















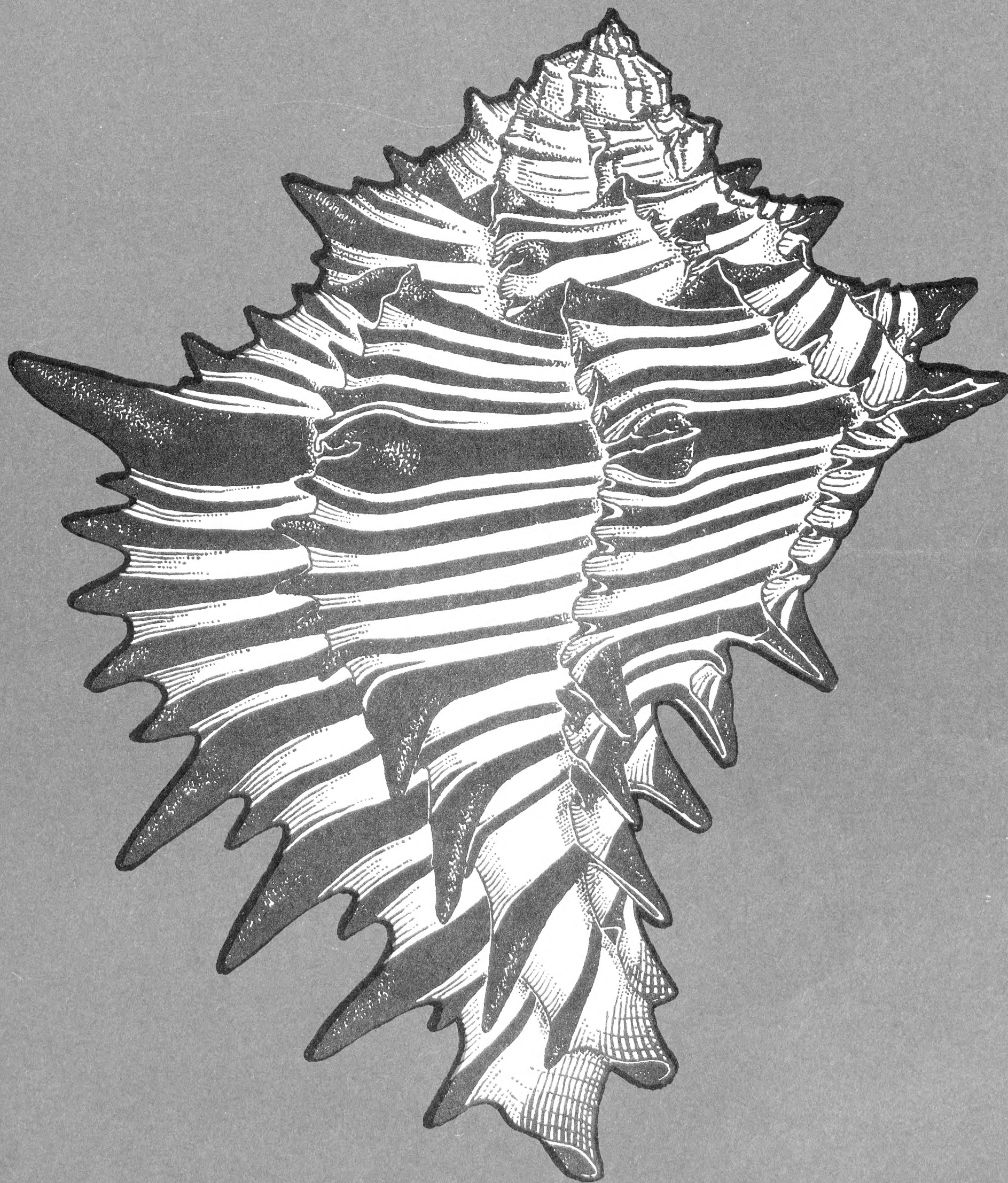
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# AN HISTORICAL REVIEW OF YORKSHIRE MOLLUSCA

A. NORRIS<sup>1</sup>

(Presidential address, delivered before the Society, 17 March 1984)

## INTRODUCTION

The Local Government Act of 1972 which created counties such as Humberside and South Yorkshire drastically changed the map of Yorkshire by altering the position of the county boundaries. For the purpose of this paper I consider Yorkshire to be the historical county as outlined by Hewett Cottrell Watson (Watson 1852, Dandy 1969).

The old county of Yorkshire was the largest of the English counties at 3,882,848 acres or 6,067 square miles. That represented 10.5% of the total land mass of England and Wales, or 5% of the British Isles. Historically the county was divided into three ridings, East, West and North Riding, from the Icelandic 'thridding', a third part. The North Sea forms the county's eastern boundary and the rest is bordered by seven counties; Durham to the north, Westmorland (now Cumbria) and Lancashire to the west, and the counties of Cheshire, Derbyshire, Nottinghamshire and Lincolnshire to the south and south-west. For the purpose of mapping Watson divided the county into five vice-counties, 61 south-east, 62 north-east and 63, 64 and 65 south-, mid- and north-west respectively.

## THE EARLIEST RECORDS

*Martin Lister*

The earliest written reference to Yorkshire mollusca is to be found in Dr. Martin Lister's *Historiae Animalium Angliae tres tractatus*, published in 1678. In this publication he gives Yorkshire localities for 14 of the land and fresh-water species he describes, as well as numerous marine species from the River Tees, Redcar, Scarborough, Philo (Filey) and the mouth of the River Humber. An appendix published in 1681 adds a further 3 freshwater species to the Yorkshire list. In an even earlier publication Dr. Martin Lister states 'And I can assure you, that of near 30 species, I have now by me, found in this county alone, not any one can be sampled by any sea, fresh-water or land-snail, that I have, or ever saw' (Lister 1674). In other words, Lister is telling us that he has found nearly 30 species in Yorkshire which he has never seen in any other area. This note in the form of a letter does not, however, give localities or distinguish land and fresh-water from marine species. Martin Lister, a physician, was resident in York from October 1670 to 1683, and it was during this period that he wrote some of his most famous books and papers (Jackson 1945). Lister also had family connections with Yorkshire, being descended from the ancient Yorkshire family of Lister from Midhope and Thornton in Craven (near Skipton). His first wife Anna was the daughter of Thomas Parkinson of the old manor house and estate at

<sup>1</sup> Leeds City Museum, Municipal Buildings, Leeds, LS1 3AA.

Carlton in Craven. Martin Lister spent many summers in Carlton and his wife subsequently inherited one third of the estate (Davies 1873).

Lister is considered to have published the first records for Britain for some 44 species of land and fresh-water Mollusca. Most of these were published in 1674 but others were published in 1678, 1681 and 1686.

Seventeen species of Mollusca with specific Yorkshire localities published by Lister in *Historiae Animalium Angliae* (1678) and the appendix, (1681) were accepted by Kennard and Woodward (1926) as the first records for Britain.

Pottery or Potteric Carr near Doncaster, now a Yorkshire Wildlife Trust Nature Reserve, leased from British Rail, must be the first locality in Yorkshire, and possibly even in Britain, to have a published list of its freshwater Mollusca. Martin Lister recorded the following fresh-water species from this locality:

*Viviparus contectus* (Millet 1813), *Lymnaea (Lymnaea) stagnalis* (L. 1758), *Anisus (Disculifer) vortex* (L. 1758), *Anodonta anatina* (L. 1758) and *Sphaerium (Sphaerium) lacustre* (Müller 1774) (Lister 1678, 1681).

The localities given for one of the species described by Lister is, however, open to question. He records that the pearl mussel *Margaritifera margaritifera* (L. 1758) was 'found in the deep pools of the River Tees in Yorkshire, not far from Dinsdaell (Dinsdaell or Dinsdale is an area bordering the River Tees south-east of Darlington). This then begs the question, how is it that the first record of this species for Britain comes from a river in which no further specimens have ever been found? J. W. Jackson in his paper on Martin Lister (1945), records *Trichia (Trichia) striolata* (C. Pfeiffer 1828) as having been described by Lister and found 'in woods and on the moist shady banks of hedges around Tadcaster; they are found in the same places plentifully in the mountain country called Craven'. Kennard and Woodward (1926) did not give any opinion as to the identity of this species as described on page 125 (No. XII) in *Historiae Animalium Angliae* but did accept the variety found in Kent as *Monacha cantiana*. It seems strange that they did not accept either *Trichia striolata* or the closely related *Trichia (Trichia) hispida* (L. 1758), and it can only be assumed that the confusion between these two species made them err on the side of caution. If J. W. Jackson is correct then this would be the first British record of *striolata* as opposed to DaCosta's record of 1778.

Martin Lister was the first person to record the presence of the red fluid secreted by *Planorbarius corneus* (L. 1758) and *Planorbis planorbis* (L. 1758). He was so intrigued by this 'red humour' that his description occupied a full page. Lister was also the first person to note the presence of the love-dart or gypsobelum in *Helix (Cornu) aspersa* Müller 1774. Charles Ashford of the Friends' School at Ackworth near Wakefield was to develop the study of these darts in a series of papers published in the Journal of Conchology between 1883 and 1885. Ashford's Collection of darts is now housed with his other collections at the City Museum in Leeds.

#### *William Bean and Ralph Thoresby*

A few scattered Yorkshire records can be found in books published by Pennant 1777, DaCosta 1778, Montagu 1803 and Donovan 1804, but it was William Bean the 2nd of Scarborough (1787–1866) who was the next in a long series of eminent Yorkshire conchologists. The main part of his collection of British land, fresh-water and marine Mollusca, mainly from the 'Scarborough area', is now housed in the Woodend Museum at Scarborough. This collection is important not only for its scientific content, but also because it is the earliest Yorkshire shell collection still in existence. William Bean was born into a family of market gardeners but he was by instinct more of a naturalist cum



entrepreneur. It was not long before he put his hand to turning the market gardens known as Bean's Gardens into pleasure gardens. These became known as the 'Subscription Promenade Gardens' or 'Vauxhall Gardens' (McMillan & Greenwood 1972). He also regularly exhibited the collection of shells at his private museum in Vernon Place, Scarborough.

In fact, this was not the first collection of Yorkshire Mollusca to be exhibited to the general public. The Museum Thoresbyanum of Leeds must take this honour (Thoresby 1715). In his *Ducatus leodiensis* Ralph Thoresby published a catalogue of his museum in which he devoted some six pages to the shells on exhibition. As well as Yorkshire material forwarded to him by Dr. Martin Lister, the catalogue gives details of material from well-known people such as Hans Sloane (1660–1753) the founder of the British Museum, and Dr. Nehemiah Grew (1628–1712), and from exotic places as far afield as Jamaica, India and Carolina.

The second edition of Theakston's Guide to Scarborough, published in 1841, gives a list of the land and fresh-water shells of the Scarborough district compiled by William Bean. One of the main difficulties encountered when looking at his collection or the published lists is to assess the extent of the area he called 'Scarborough'. It is well known that some of the material, land, fresh-water and marine, could not have been found within many miles of Scarborough. *Pseudamnicola confusa* (Frauenfeld 1863) (= *Paludina similis*) and *Lacinaria (Alinda) biplicata* (Montagu 1803) (= *Clausilia biplicata*), both appear in this list of Scarborough species, but as they are unknown north of the Wash they should not have found their way onto a list of Yorkshire Mollusca.

Although William Bean dominated the Yorkshire scene in the early half of 19th century, it must be remembered that a great deal of important work was being done on the Mollusca by contemporaries such as Joshua Alder (1792–1867), A. Hancock (1806–1873) and John Gwyn Jeffreys (1807–1885).

## 19TH AND 20TH CENTURIES

### *The Learned Societies*

The foundation of many Literary and Philosophical Societies in the earlier part of the 19th century (Leeds 1818, Sheffield 1822, Bradford, Whitby and York 1823, Wakefield and Scarborough 1827 and Halifax 1830), (Brears 1984), as well as Mechanics' Institutes saw a dramatic increase in the study of conchology. As early as 1837 the Leeds Philosophical and Literary Society published detailed accounts of the anatomical examination of slugs, (Nunneley 1837). This type of paper had previously only been published in such periodicals as the Zoological Journal. Also, by the establishment of permanent museums the Literary and Philosophical Societies encouraged collecting of all types of man-made and natural objects. The establishment of these museums reflected a growing interest in man and his environment largely as a result of world exploration and the establishment of a colonial empire. Curators were appointed to look after these collections and to liaise with explorers, missionaries and military expeditions, as well as freelance dealers and collectors. The early records of these societies reflect the hunger for material from both local and exotic localities.

The first of the local natural history societies was the Huddersfield Naturalists' Society, founded in 1847 (Crackles 1984) but it was the foundation of The West Riding Consolidated Naturalists' Society at Heckmondwike in September 1861, which did most to change the face of natural history in Yorkshire, as this federation of societies subsequently became The Yorkshire Naturalists Union. The Union's publication, The Naturalist, was



first published in 1875 but two earlier publications, *The Naturalist* (1864–1867) and *The Yorkshire Naturalists' Recorder* (1872–1873) were produced by the West Riding Consolidated Naturalists' Society.

Many of the member societies of the Union also produced their own publications, and thus from the mid 1860s to the beginning of the Great War, Yorkshire produced a large number of local natural history journals. This period also produced a large number of conchologists. Some, like H. T. Soppitt and J. W. Carter (1888), Charles Ashford (1874) and Fred Booth (1921) published very local faunas, adding greatly to our knowledge of the mollusca of Yorkshire. T. Petch (1904), however, was the only person to produce a vice-county fauna with his coverage of the land and fresh-water Mollusca of the East Riding. Reports on the marine Mollusca were also produced by W. C. Hey (1884) and F. H. Woods (1912). An attempt to compile a faunal list of the land and fresh-water Mollusca of Yorkshire was made by W. Nelson and J. W. Taylor in a series of papers published in the *Transactions of The Yorkshire Naturalists' Union* between 1877 and 1891, but this was never completed. The only county fauna which has ever been produced covering land, fresh-water and marine species is that published in the *Victoria County History* in 1907. However, it was not until much later that Walsh and Rimington (1956) produced the most useful publication on Yorkshire Mollusca with the production of the *Natural History of the Scarborough District*, a compilation of all published records for the area.

The most important event that took place during this period, as far as this society is concerned, was the publication of the *Journal of Conchology* in 1874. This led to the foundation of the Conchological Society of Great Britain and Ireland in 1876. A great deal has been written about the four founding members, John W. Taylor (1845–1931), W. Denison Roebuck (1851–1919), Henry Crowther (1848–1937) and William Nelson (1835–1906), and the foundation of this society (Crawley 1975) and the Yorkshire Conchological Society (Norris 1982). I do not wish, therefore, to dwell any further on this aspect of the story.

I would like to mention, however, that William Nelson's collection of land and freshwater shells were purchased from his widow by the membership of the Yorkshire Naturalists' Union, as it was felt that this would be the best way to help his family financially, as well as ensuring the future existence of this important collection. The Union presented the collection to Leeds University; however it has since been transferred into the care of the Leeds City Museum.

The presence of the collection at Leeds University may have influenced Prof. Walter Garstang (1868–1949) who took up the chair of zoology at Leeds University in 1907, to become involved with both The Yorkshire Naturalists' Union and The Yorkshire Conchological Society. It is almost certain that it was Walter Garstang who recommended all three of the surviving founder members of The Conchological Society for honorary degrees. Prof. Garstang published a large number of papers in his lifetime but he is probably best known for his little book entitled *Larval Forms and other Zoological Verses* published by Blackwells of Oxford in 1951. These verses are still used by students as 'aide memoires' as they are scientifically correct. 'The Ballad of the Veliger or How the Gastropod got its twist' written in 1928 is perhaps one of the best of these.

The following is a short extract from this ballad.

#### The Ballad of the Veliger or How the Gastropod got its Twist

The Veliger's a lively tar, the liveliest afloat,  
A whirling wheel on either side propels his little boat;  
But when the danger signal warns his bustling submarine,  
He stops the engine, shuts the port, and drops below unseen.

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He's witnessed several changes in pelagic motor-craft;  
The first he sailed was just a tub, with a tiny cabin aft.  
An Archi-mollusk fashioned it, according to his kind,  
He's always stowed his gills and things in a mantle-sac behind.

Young Archi-mollusks went to sea with nothing but a velum –  
A sort of autocycling hoop, instead of pram – to wheel 'em;  
And, spinning round, they one by one acquired parental features,  
A shell above, a foot below – the queerest little creatures.

Yorkshire has produced many interesting records, and some very interesting characters, and no review would be complete without mentioning some of these.

### *Greevz Fysher*

Greevz Fysher (1845–1931), was a true nineteenth century entrepreneur as the owner and managing director of Kingfisher Lubrications of Meanwood Road, Leeds. His real entrepreneurial energy, however, was aimed at his wide range of non-business interests. Fysher was an active member of a large number of pressure groups and propaganda organisations such as the Personal Rights Association, the Anti-Compulsory Vaccination Society, the Liberty Property Defence League, the Womans Franchise League, the Womans Emancipation Union and the League of Liberals against Aggression and Militarism, as well as many more (Buckman 1969 ms). He also considered himself to be 'the poor man's advocate' fighting against the tyranny of compulsion be it compulsory education, government, taxation, or customs regulations. He even considered that the act to prevent children working in factories and mines was an infringement on personal liberty. Some of his eccentricities can be seen in the following quotations taken from Buckman (1969 ms). The first relates to the rules concerning compulsory religious education in board schools. 'There was not even agreement as to what constituted the Bible, Catholics considered the Protestant version incorrect; Jews objected to the New Testament whilst Freethinkers objected to both Testaments. The Bible was, in any event, 'an unfit book' for children. It contained records of 'the foulest crimes and vices'. In 300 chapters there were words of 'indecent signification', stories of 'filthy and revolting immorality', and 'records of barbarous deeds, bloodthirsty wars, treachery, and assassination'. Fysher had very liberal and 'progressive' views about the involvement of both the church and the state in marriage. He considered an official wedding to be solely a 'secure formal record of a natural union' and that the registrar should only be reluctantly tolerated. He could see no reason why a beneficial custom should become law. Free marriage would, he said, be 'nobler and quite as useful'. He also considered the wedding ring to be a 'degrading superstition and servile subjection to the woman', and that 'any movement for the facilitation of divorce' was a step in the right direction'.

Fysher was perhaps most famous in Yorkshire for his letters. As a great believer in spelling reform he wrote phonetically, developing a script which he considered could be used by printers without any change in type-faces. The following is a short extract taken from a letter sent to the Newcastle Chronicle, 5th December 1891.

Ser, Ei hav seen a gwd propoarshun ov dhe korespondens hwich haz reesentli apeerd in ewr kolumz, and ei wd hav riten tw ew befoar had ei not been so bizily okewpeid in odher waiz. Ei thngk spelling reformerz hav sum kawz tw komplain dhat wun hoo noaz az much az Mr.



Eizack Pitman duz ov dhis subjekt shwd reit az dho dhair iz no noan method ov speling ewzabel bei ordinari printerz widhowt dhe employment ov eni new teips, and bei hwich dhe pronunsiaishun ov eech wurd kan be represented widh a fair aproximaishun tw akewrasi. Such a sistem iz eksemplifeid (baring aksidental eror) in dhis letter.

### *King Lane Pond*

Perhaps the most famous record that has ever come out of Yorkshire was the discovery of a thriving colony of sinistral *Lymnaea (Radix) peregra* (Müller 1774) in a pond off King Lane in Leeds. This is a good record to discuss as it brings into focus many of the characters involved over the years. Although the pond no longer supports this form it is still in existence and a great deal of work has recently been undertaken by the present owners to restore it to its Victorian splendour. Surprisingly, however, the genetic stock of left-handed *peregra* still exists in the laboratories of the University of Texas (J. Lundelius pers. comm.). The sinistral monstrosity was originally noticed in the pond by William Nelson in May 1901 (Nelson 1901). It was Prof. Boycott, however, who set the wheels in motion to preserve the colony in what became known as King Lane Pond. Lord Moynihan, the landowner, had sold off the area containing the pond to developers after the laying of Scott Hall Road had divided it off from the remainder of his estate. (Fysher 1931). The developers, wishing to keep the pond as a feature of the new estate, incorporated it into the design scheme. I have no doubt that the action of the developers resulted from the interest expressed in the pond by the conchologists of the time. It was Greevz Fysher, however, in co-operation with John W. Taylor, who undertook all the negotiations with Sir Berkeley Moynihan, as he was then known, and the developers Messrs. A. & F. Mosley. The pond was re-shaped from a rough rectangle into a formal circle with an ornate iron fence around it, Boycott himself having approved the landscape design. The area of the pond was subsequently divided up into equal parts like the slices of a cake and sold as part of the plots on which the surrounding houses stood. Attempts were also made to control the numbers of *Lymnaea (Lymnaea) stagnalis* (L. 1758) by collecting them in large numbers for destruction.

Greevz Fysher was not the only noted Yorkshire conchologist to surround himself with controversy. John W. Taylor, one of our founding fathers, had some very controversial theories. A paper delivered to this Society proved to be so controversial that the Society refused to publish it. The following, a small extract from the manuscript, now in my private collection, relates to the dominance of Europeans over other races, 'The Master Race Theory'. The plates referred to in the text are part of the collection of books, illustrations and slides acquired from the late Miss Taylor which are now housed in the City Museum, Leeds.

'The European or white race of man kind as in other classes of life is superior to every other race which is multiplying rapidly extending its dominion over the inferior races (pl. XI fig 11.). The Mongolian or Yellow race is now subdominant only and is admittedly inferior in intellect, in influence and dominating power to the European who is gradually encroaching upon the territories they possess. (pl. X fig. 9)'.

The above extract requires no further comment and Taylor's views must have been just as incorrect and unacceptable then as they are today.

John Armitage, the present President of the Yorkshire Conchological Society, has been involved with King Lane Pond since his appointment as Keeper of Natural History at the Leeds City Museum back in 1952. His connection with the Conchological Society has been

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long but sporadic, his first contacts dating back to his early teens. As a close friend of Fred Taylor of Oldham he developed a deep interest in ornithology, photography and journalism as well as conchology. Trained as an artist at the Oldham School of Art, his skill was such that at the age of 15 whilst working for Messrs. T. Oliver, Illuminating Artists of Manchester, he designed and produced the Illuminated Address presented by this Society to Mr. John W. Taylor on the occasion of his 70th birthday, (See J. Conch. **14**: 316–319), in 1915. It is mainly because of John Armitage's enthusiasm and guidance that the Yorkshire Conchological Society is as healthy as it is today.

## PRESENT STATUS OF YORKSHIRE MOLLUSCA

Although sometimes surrounded by controversy, these and many other Yorkshire naturalists have left us with a richly documented fauna. The total number of land and fresh-water Mollusca records for the county at the present time is 158 species, that is 81% of the British species. Two of these have become extinct within the county since records began. The two, both fresh-water gastropods, *Myxas glutinosa* (Müller 1774) and *Segmentina nitida* (Müller 1774) have become much rarer generally in recent years and may be on the verge of extinction as British species. With regard to the marines, over 350 species of marine Mollusca have been recorded for Yorkshire in the past 300 years. This number of species is reduced, however, in the Sea Area Atlas of the Marine Molluscs of Britain and Ireland, (Seaward 1982), which has published maps for 746 British species. Sea Area 11 which covers most of the Yorkshire coast is shown as having 163 live records post-1950, 45 live records pre-1951, and a further 83 records based on shells alone, making a total of 291 species. The discrepancy of over 60 species is partly a result of over-enthusiasm on the part of William Bean and others, and partly due to advances in our knowledge of distribution patterns which has resulted in numerous questionable species having to be removed from the Yorkshire list. Robin Hood's Bay has proved to be the most productive locality on the Yorkshire coast, but this is mainly due to the presence of the Wellcome Marine Laboratories which housed a number of research students working on this group of animals. The most outstanding of these was Chris Todd who, over the years, added a large number of sea slugs to our faunal list. It is most regrettable that financial constraints have recently forced the University of Leeds to close the laboratories, and thus to curtail the long and steady development of conchology in the county of Yorkshire.

## ACKNOWLEDGEMENTS

No review of the Mollusca of Yorkshire could possibly have been undertaken without the vast quantity of information gathered together by the various recorders and members of the Conchological Society of Great Britain and Ireland, the Yorkshire Conchological Society and the Yorkshire Naturalists' Union. I would like to thank all these people, past and present, for the help they have given in the production of this paper. In particular I would like to thank Mr. T. L. Blockeel for translating some of the publications of Dr. Martin Lister, Mr. Paul Howard of the Yorkshire Museum, Gena Douglas, Librarian at the Linnean Society, Mr. K. D. Versey of Kingfisher Lubrications, Leeds, and Mr. Tom Pain. My thanks are also due to the staff of the City Museum and the Local History Library at Leeds, and last, but not least, to my wife Barbara for reading the manuscript and for all her help and assistance in the production of this address.



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# THE TAXONOMIC STATUS OF *LITTORINA TENEBROSA* MONTAGU AS ASSESSED BY MORPHOLOGICAL AND GENETIC ANALYSES

K. JANSON<sup>1</sup> AND R. D. WARD<sup>2</sup>

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**Abstract:** Swedish populations of the small brackish-water periwinkle *Littorina tenebrosa* were examined over a micro-environmental cline. Canonical variate analysis of shell parameters showed a gradual change from typical *L. tenebrosa* phenotypes to those resembling specimens of *L. saxatilis* from sheltered boulder shores. At the gene-allozyme level, the Swedish populations of *L. tenebrosa* were almost identical with nearby *L. saxatilis* populations, giving a genetic identity of about 0.99. A comparison of Scottish populations of *L. tenebrosa* with nearby *L. saxatilis* gave similarly high identities. It is concluded that *tenebrosa* is a distinct form of *L. saxatilis* rather than a species in its own right. The ecotype concept is discussed with reference to the various forms of *L. saxatilis* and it is recommended that this term be applied to the various ecologically distinct morphs of *L. saxatilis* in preference to such terms as subspecies or races.

## INTRODUCTION

In recent years, morphological and biochemical genetic studies have identified four species in the *L. saxatilis* species complex (reviewed by Raffaelli 1982). These species are: *L. saxatilis* Olivi (= *L. rudis* Maton), *L. arcana* Hannaford Ellis, *L. neglecta* Bean, and *L. nigrolineata* Gray. However, the taxonomic status of *L. tenebrosa* Montagu has not been thoroughly investigated, although it has been suggested that it might be a distinct species within the *saxatilis* complex (Muus 1967, Fretter & Graham 1980, Smith 1982).

*L. tenebrosa* is found in sheltered lagoons or bays with reduced salinity, living on sea plants such as *Zostera marina* (L.) and algae, or on the soft muddy bottom. It prefers submerged conditions rather than the littoral or supra-littoral zones occupied by the other saxatilids. It lives in brackish waters of salinities down to 7–8, although high numbers are found in salinities above 10‰ (Muus 1967).

Undoubtedly, *L. tenebrosa* is more closely related to *L. saxatilis* itself rather than any of the other saxatilids listed above. The two species are, for example, similar in mode of reproduction and in morphology of the soft parts (Fretter & Graham 1980). The differences between *tenebrosa* and *saxatilis* are in the shell characteristics, *tenebrosa* shells being smaller, thinner and darker in colour than shells of *saxatilis*. However, it should be remembered that *L. saxatilis* is a highly variable species, with significant differences in shell characters between groups of snails inhabiting, for example, exposed and sheltered habitats (Janson 1982a), and it shows abundant colour polymorphism (Atkinson & Warwick 1983).

In this study, we have analysed morphological variation within *tenebrosa* and *saxatilis* populations from Sweden, and have compared enzyme patterns of *tenebrosa* and *saxatilis* within and between two geographically separated areas in Sweden and Scotland. We conclude from the results that *L. tenebrosa* is but another phenotype of the species *L. saxatilis*.

<sup>1</sup> Tjärnö Marine Biological Laboratory, P.O. Box 2781, S-452 00 Sweden

<sup>2</sup> Department of Human Sciences, Loughborough University of Technology, Loughborough, Leicestershire, LE11 3TU



## MATERIALS AND METHODS

The Scottish populations were from Oban a'Chlachain (Ordnance Survey map reference: NF 820638) on North Uist, Outer Hebrides. Specimens of *tenebrosa* were living submerged on fucoid algae and stones in the most sheltered part of a small inlet from the Atlantic, while the *saxatilis* occupied stones at the edge of the inlet. The *tenebrosa* individuals were much smaller than the *saxatilis* and uniformly blackish in colour. Many colour morphs were present in the specimens of *saxatilis*.

The Swedish populations were from the area around the Tjärnö Marine Biological Laboratory on the Swedish west coast. The *saxatilis* population inhabits the littoral zone of the west-facing shore of the island of Saltö. This population had earlier been found to be morphologically variable, with small, thin-shelled, large-apertured forms (*E*) inhabiting the exposed cliffs and large, thick-shelled, small-apertured forms (*S*) living in adjacent sheltered boulder bays (Janson 1982a). The *E* and *S* morphs intergrade (Janson and Sundberg 1983) and allozyme analysis verifies that they belong to the same species (Janson & Ward 1984). The *tenebrosa* population sampled inhabits a shallow soft-bottomed bay 2 km north-east from Saltö. The snails typically live submerged, on or among plants of *Zostera marina*. They are darker and less variable in colour than the *saxatilis* phenotypes.

Shell morphologies of 29 to 34 specimens of Swedish *tenebrosa* and *saxatilis* phenotypes were compared with a multivariate technique, canonical variate analysis, on five shell measurements; length (*L*), width (*W*), aperture length (*AL*), aperture width (*AW*), and weight (*WE*). These measurements were transformed into the parameters:  $A(=W/L)$ ,  $B(=AL/L)$ ,  $C(=AW/L)$ , and  $D(=(WE/L^3) \times 1000)$  to avoid differences between samples due to size discrepancies. Details and references on the method are given in Janson & Sundberg (1983). One sample of each phenotype of *saxatilis*, *E* and *S*, and three samples of *tenebrosa*, *T1*, *T2*, and *T3*, were analysed. The *tenebrosa* samples were from a micro-environmental gradient; *T1* from the real mud-flat, *T3* from small boulders on the edge of the shallow bay (thus representing an atypical *tenebrosa* habitat), and *T2* from a site between *T1* and *T3*. From *T1* to *T3* it was only 5 m.

The allozyme patterns of *tenebrosa* and *saxatilis* from Scotland and Sweden were compared by means of starch gel electrophoresis. Four groups of specimens were considered: *saxatilis* and *tenebrosa* from North Uist ('SCOSAX' and 'SCOTEN' respectively), and *saxatilis* and *tenebrosa* from the Saltö area ('SWESAX' and 'SWETEN' respectively). Allele frequencies were calculated from observed genotype numbers, the allele frequencies of SWESAX being averages of the frequencies found in 11 subpopulations located over a 1 km stretch of Saltö coastline. These SWESAX data are presented in full in Janson & Ward (1984), and include both *E* and *S* phenotypes. SWETEN was from the *T1* population. Between 19 and 23 loci were scored in 11 to 55 specimens (average 30.0) of each group using the same methods, and locus and allele designations as in Ward & Warwick (1980) and Janson & Ward (1984). Breeding tests on many of the polymorphic loci have confirmed the genetic interpretations assigned to the observed banding patterns (Warwick & Ward unpublished).

## RESULTS

*Shell morphology*

The means and standard deviations of the shell length (*L*) and the four parameters (*A*, *B*, *C*, and *D*) of the different samples are given in Table 1. Projections of canonical variables

TABLE 1

Means and standard deviations of shell length (*L*), and of four shell parameters (*A*, *B*, *C*, and *D*) which represent size independent transformations of width, aperture length, aperture width, and shell weight, respectively (see text for details) of three *tenebrosa* (*T1*, *T2*, and *T3*) and two *saxatilis* (*S* and *E*) samples from Sweden.

	<i>T1</i>	<i>T2</i>	<i>T3</i>	<i>S</i>	<i>E</i>
	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)
<i>L</i> (mm)	4.79 (1.01)	5.28 (1.38)	8.45 (2.55)	8.14 (0.71)	4.81 (0.91)
<i>A</i>	0.89 (0.03)	0.89 (0.04)	0.86 (0.03)	0.88 (0.03)	0.95 (0.02)
<i>B</i>	0.65 (0.04)	0.68 (0.04)	0.69 (0.05)	0.76 (0.02)	0.78 (0.02)
<i>C</i>	0.47 (0.02)	0.47 (0.03)	0.45 (0.03)	0.49 (0.02)	0.59 (0.04)
<i>D</i>	0.62 (0.13)	0.82 (0.15)	0.87 (0.12)	0.96 (0.08)	0.51 (0.05)
<i>n</i>	33	34	34	31	29

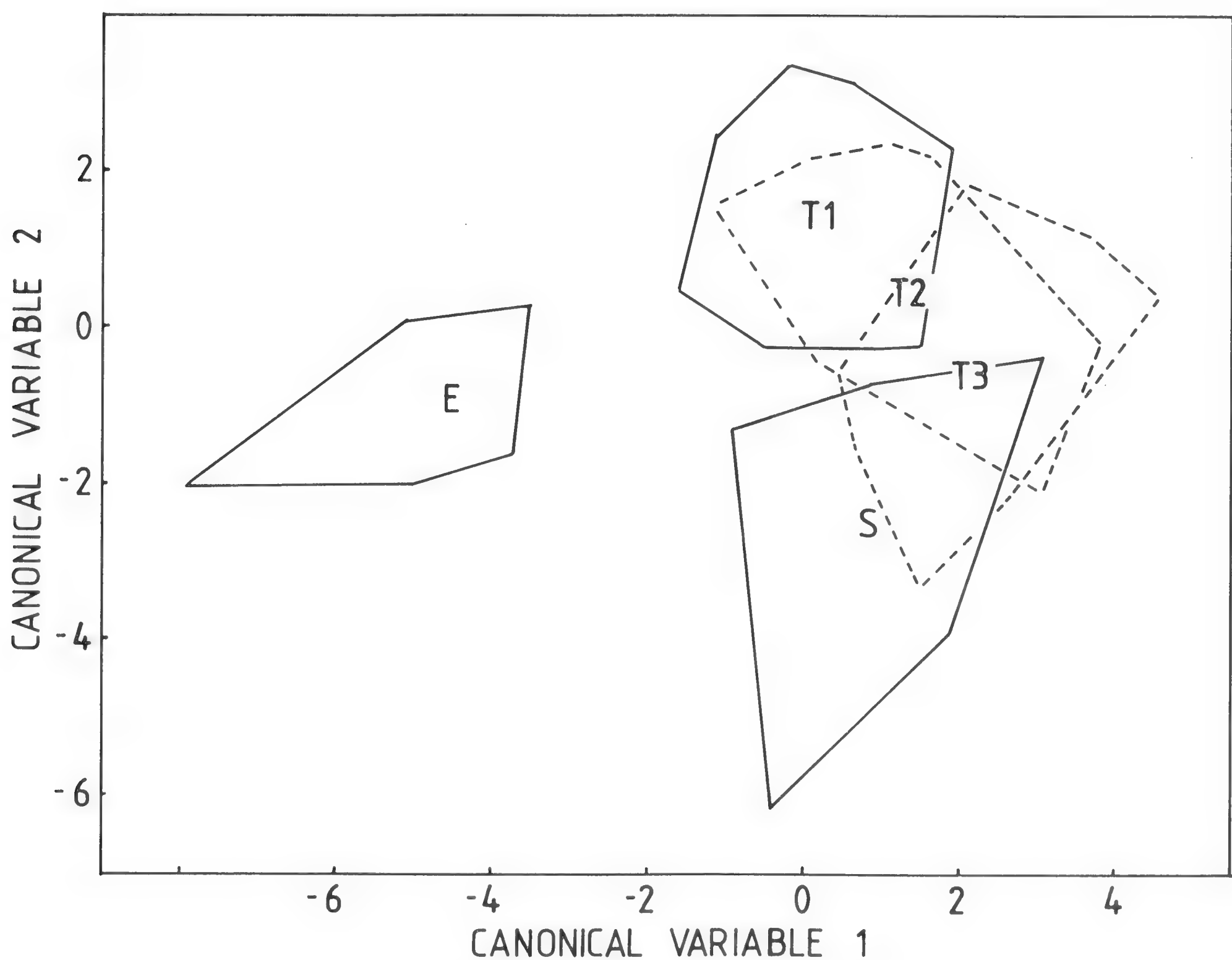


Fig. 1. Position of *tenebrosa* (*T1*, *T2*, and *T3*) and *saxatilis* (*S* and *E*) samples in the projection of the first two canonical variables estimated from shell measurements. Letters indicate coordinate means of each sample and lines enclose individuals within each group.



TABLE 2

Genetic variation in populations of *L. saxatilis* from Scotland (*SCOSAX*), and from Sweden (*SWESAX*), and in *L. tenebrosa* from Scotland (*SCOTEN*), and Sweden (*SWETEN*).

Locus	allele	<i>SCOSAX</i>	<i>SCOTEN</i>	<i>SWESAX</i> *	<i>SWETEN</i>
<i>Sdh</i>	100	1.000	1.000	0.954	1.000
	50	—	—	0.046	—
	N	24	17	20.1	26
<i>Idh-2</i>	100	1.000	1.000	0.926	0.968
	75	—	—	0.074	0.032
	N	26	25	35.5	31
<i>Odh</i>	105	0.851	0.792	0.886	1.000
	100	0.149	0.208	0.114	—
	N	37	24	26.9	44
<i>Sod-1</i>	105	—	—	0.008	—
	100	1.000	1.000	0.862	0.975
	90	—	—	0.130	0.025
<i>Aat-1</i>	N	14	22	19.3	20
	120	—	—	0.255	—
	100	1.000	1.000	0.745	0.981
<i>Aat-2</i>	90	—	—	—	0.019
	N	25	22	40.4	54
	150	0.060	0.050	0.011	not scored
<i>Pgm-F</i>	100	0.940	0.950	0.989	0.909
	N	25	22	30.8	11
	100	0.870	0.967	0.956	0.909
<i>Pgm-1</i>	95	0.130	0.033	0.044	0.091
	N	23	15	30.2	11
	105	0.057	0.077	0.052	—
<i>Pgm-2</i>	100	0.750	0.756	0.673	0.857
	85	0.193	0.167	0.274	0.143
	75	—	—	0.001	—
<i>Est-1</i>	N	45	39	41.3	28
	100	0.534	0.346	0.422	0.577
	85	0.455	0.590	0.572	0.404
<i>Lap-1</i>	70	0.011	0.064	0.006	0.019
	N	44	39	43.5	26
	105	—	—	0.005	—
<i>Lap-2</i>	100	1.000	1.000	0.995	1.000
	N	39	39	37.0	54
	110	0.154	0.026	—	—
<i>Ap</i>	105	0.051	0.038	0.005	—
	100	0.795	0.936	0.974	1.000
	85	—	—	0.021	—
<i>Mpi</i>	N	39	39	37.7	20
	100	1.000	1.000	0.996	1.000
	85	—	—	0.004	—
<i>Mpi</i>	N	39	39	39.5	43
	110	0.083	0.047	0.004	0.019
	100	0.917	0.953	0.969	0.944
<i>Mpi</i>	85	—	—	0.027	0.037
	N	30	32	34.2	54
	130	—	—	0.003	—
<i>Mpi</i>	120	0.339	0.343	0.688	0.619
	100	0.661	0.656	0.309	0.381
	N	31	32	35.1	31

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TABLE 2 (CONTINUED)

Locus	allele	SCOSAX	SCOTEN	SWESAX*	SWETEN
<i>Pgi</i>	110	—	—	0.008	0.009
	100	0.883	0.859	0.644	0.778
	90	0.117	0.141	0.341	0.213
	80	—	—	0.007	—
	N	30	32	48.3	54
$\bar{H}_I$		0.110	0.097	0.127	0.105

Monomorphic loci: *Ak*, *Ldh*, *Mdh-1*, *Mdh-2*, *G6pdh*, *Idh-1*, *Xdh*, and *Hdh*. (However, *Ak*, *Mdh-2*, and *Idh-1* were not scored in *SWETEN*.)  $N=13-37$ ,  $\bar{N}=25.1$

\* Average of 11 subpopulations within 1 km, calculated from Janson and Ward (1984).

TABLE 3

Genetic identities (*I*, above diagonal) and distances (*D*, below diagonal) between pairs of the populations.

	SCOSAX	SCOTEN	SWESAX	SWETEN
SCOSAX		0.996	0.980	0.990
SCOTEN	0.004		0.983	0.989
SWESAX	0.020	0.017		0.990
SWETEN	0.010	0.011	0.010	

Average allele frequencies for Swedish *saxatilis* (SWESAX) calculated from Janson & Ward (1984).

1 and 2 (which accounted for 97.1% of the total dispersion within the samples) showed that the sample of *tenebrosa* from the typical *tenebrosa* habitat, *T1*, was clearly distinct from both the *E* and *S* phenotypes of *saxatilis*. However, over the micro-environmental cline (*T1*→*T2*→*T3*), the *tenebrosa* phenotype gradually changed towards the *S* phenotype of *saxatilis* (Fig. 1).

### Allozyme analysis

Allele frequencies in the four groups of snails (*SWETEN*, *SWESAX*, *SCOTEN*, and *SCOSAX*) are given in Table 2. Differences in allele frequencies between the groups are small, with only one locus, *Mpi*, showing any clear differentiation. At this locus, the allele *Mpi*<sup>120</sup> is the most common in both Swedish samples while the allele *Mpi*<sup>100</sup> is the most common in the North Uist populations.

Estimates of Nei's (1972) genetic identity and distance emphasise the close genetic relationship between all four groups, the mean genetic identity between *tenebrosa* and *saxatilis* being around 0.99 (see Table 3). UPGMA cluster analysis (Sokal & Sneath 1963) shows that Swedish *tenebrosa* and *saxatilis* are in fact more similar to each other than either is to their Scottish counterparts, and the same is also true with regard to the Scottish *tenebrosa* and *saxatilis* (Fig. 2). Thus the limited genetic differentiation between populations reflects geographic separation and there is no evidence of any intrinsic barriers to gene flow between *tenebrosa* and *saxatilis*.



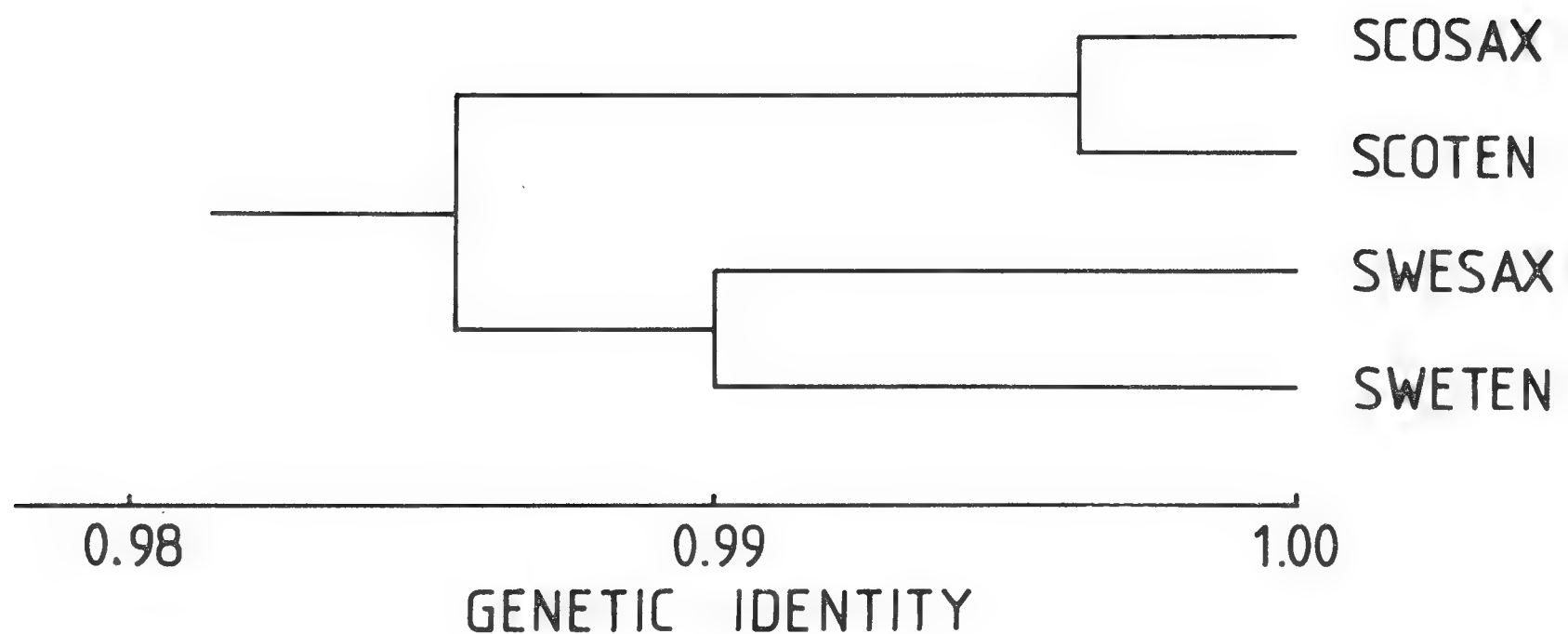


Fig. 2. Cluster analysis (UPGMA) of genetic identities ( $I$ ) between samples of *saxatilis* and *tenebrosa* from Scotland and Sweden.

#### DISCUSSION

The conclusion arising from the morphological and genetical analyses of this study is that the form *tenebrosa* belongs to the species *L. saxatilis* and is not a species in its own right. This conclusion is supported by three observations. Firstly, the genetic identities between *tenebrosa* and *L. saxatilis* populations (0.983–0.996) are very high, and are well above what is already an extremely high  $I$  value of the two sibling species *L. arcana* and *L. saxatilis*, 0.957 (Ward & Warwick 1980). Secondly, genetic differentiation of populations is governed more by geographical distance than by whether morphs have the *tenebrosa* or *saxatilis* shell phenotype. Thirdly, although the *tenebrosa* form is phenotypically distinct from other *saxatilis* morphs, microgeographical variation of morphs along an environmental cline exhibits transitional zones rather than overlapping distributions of the different phenotypes. In this way, the *tenebrosa* morph parallels other phenotypes (e.g. exposed, *E*, and sheltered, *S*, morphs) within the species *L. saxatilis*.

It has been shown that a genetic difference in growth rate exists between the *E* and *S* phenotypes (Janson 1982b), and breeding data indicate that most shell characters are inherited (Janson & Warwick personal observations). Thus it is likely that the particular shell morphology of the *tenebrosa* phenotype is, at least to some extent, genetically determined. The relatively sedentary life of juvenile and adult *L. saxatilis*, together with the lack of a pelagic larval stage, results in a restricted exchange of genes between subpopulations that might be only metres apart (Janson & Ward 1984). This promotes the establishment of adaptively superior genotypes in local populations, and since shell morphology appears to be an important component of fitness in *L. saxatilis* (Raffaelli 1978, Janson 1983), it is expected to vary between populations in response to varying environmental pressures. This potential for local adaptation perhaps explains why *L. saxatilis* is able to occupy such a broad range of habitats, ranging from exposed rocks and sheltered shores in the littoral zone to a sub-littoral life in brackish-water, soft-bottomed lagoons.

Smith (1980) and Fretter & Graham (1980) used the term 'ecomorph' in taxonomic discussions of the status of *tenebrosa*. 'Ecomorph' is clearly a synonym of 'ecotype' (Turesson 1922), a term mainly used with respect to the population ecology of plants. As reviewed by

Futuyma (1979), the ecotype concept includes: 1) clinal variation over very short transects, 2) the same pattern of variation over corresponding environmental ranges, 3) phenotypic differences being to a minor or greater extent genetically determined, and 4) a mosaic distribution of the different ecotypes resulting from a heterogeneous environment. The species *L. saxatilis* fits well into this concept, and we accordingly recommend that the different phenotypes such as *tenebrosa*, *E*, and *S*, be called 'ecotypes' (or 'ecomorphs') rather than 'subspecies', 'races', or 'infrasubspecies' (see, for example, Smith 1982). These latter terms imply that gene flow between populations of the same phenotype is greater than gene flow between populations of different phenotypes, and this seems not to be the case in *L. saxatilis*.

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# *OXYCHILUS (ORTIZIUS?) CLARUS* (HELD) ON CORSICA AND NEW DATA ON THE SYSTEMATIC POSITION OF *HELIX HYDATINA* ROSSMÄSSLER (PULMONATA: ZONITIDAE)<sup>1</sup>

F. GIUSTI,<sup>2</sup> D. T. HOLYOAK<sup>3</sup> AND G. MANGANELLI<sup>2</sup>

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**Abstract:** The presence of *Oxychilus (Ortizius?) clarus* (Held) on Corsica is reported for the first time. Anatomical study has confirmed that, although distinct, this species is close to *O. (Ortizius?) perspectivus* (Kobelt) of southern Italy. Comparisons are given with *O. hydatinus* (Rossmässler), which is placed in a separate subgenus *Mediterranea* Clessin 1880 with *Riedelius* Hudec 1961 as a junior synonym.

## INTRODUCTION

During a visit to Corsica in April 1977 DTH collected some shells of a small *Oxychilus* which appeared difficult to identify. These were found in the woods near Bocognano (600 m) and in the Forêt de Vizzavona (900 m) (Holyoak 1983). The small size and whitish colour of the shells limited the number of taxa with which to compare these Corsican specimens. Indeed, in south-western Europe, Italy, Sardinia and Corsica only three species were known with more or less similar shell form: *Oxychilus hydatinus* (Rossmässler), *Oxychilus perspectivus* (Kobelt) and *Oxychilus clarus* (Held). The first, a widespread Mediterranean species present also in various localities on Corsica, seemed sufficiently different in its larger shell, larger number of whorls, narrower umbilicus and its less expanded body-whorl. The second and the third species, respectively known from southern Italy and from the Alps, southern France and the Pyrenees, appeared more similar, with a whitish shell and broad umbilicus. Anatomical study was thus required for identification. In the meantime, Holyoak (1983, p. 242) listed this *Oxychilus* as undetermined and possibly new.

Recently two of us (FG, GM) have found two living specimens near Bocognano, which have allowed anatomical study and provided enough data to identify the species as *Oxychilus (Ortizius?) clarus* (Held). This species has been found alive only a few times and described anatomically only once (Forcart 1957, p. 125, f. 13), so a description of the Corsican specimens is given here, along with comparisons with *O. hydatinus* (Rossmässler) and *O. perspectivus* (Kobelt).

## *OXYCHILUS (ORTIZIUS?) CLARUS* (HELD)

*Helix clara* Held 1837. Isis, **12**, p. 901.

*Hyalinia (Polita) clara*, Westerlund 1886. Fauna, **1**, p. 43.

<sup>1</sup> NOTULAE MALACOLOGICAE, XXXII. (Research on the Sardinian and Corsican Malacofauna, V). Research supported by a CNR grant ("Gruppo di Biologia Naturalistica").

<sup>2</sup> Institute of Zoology, University of Siena, Via Mattioli 4, I-53100 Siena, Italy.

<sup>3</sup> Department of Geography, University of Nottingham, Nottingham, NG7 2RD.



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*Retinella (Aegopinella) clara*, Alzona 1971. Atti Soc. It. Sc. nat. Mus civ. St. nat. Milano, **111**, p. 124.  
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*Oxychilus (Ortizius) clarus*, Kerney, Cameron & Jungbluth 1983. Landschnecken N. Mitteleurop., pp. 169–170, t. 10, f. 4a–c.  
*Oxychilus (Ortizius?)* sp., Holyoak 1983. J. Conch., Lond., **31**, p. 242.

### Description

Shell (Plate 1 A and B) small, depressed, convex above, finely striated radially, thin and transparent, glossy and whitish. The umbilicus is wide (circa 1/3 of the maximum diameter of the shell) and deep so that it is possible to see the coiling of the spire. Spire composed of  $3\frac{3}{4}$ – $4\frac{1}{4}$  whorls, expanding slowly and regularly, separated by a distinct suture. The last whorl is more expanded near the aperture, and scarcely descending. The aperture is oval and slightly oblique; the peristome is simple and unreflected and has thin and fragile margins. Maximum diameter 4–4.6 mm; height 1.75–2 mm; aperture diameter 1.75–2 mm; aperture height 1.5–1.6 mm; umbilicus diameter 1.5–1.8 mm.

The genital apparatus follows the typical *Oxychilus* scheme (Figs. 1A and B). The hermaphrodite gonad is connected by the first hermaphrodite duct to the talon (=fertilisation chamber and seminal receptacles complex). The talon is located on the inner side of a large albumen gland and communicates with the second hermaphrodite duct (=ovispermiduct). This last shows on one side a well developed and multilobed uterine portion and, on the other, a shorter and simpler prostatic portion. A short, but wide, uterine duct (=free oviduct) leads to the vagina. The first half of the vagina is enveloped by the vaginal gland. From the base of the vagina a fairly long canal rises, leading to an oval bursa copulatrix (=gametolytic gland) which lies on one side of the ovispermiduct. A thin vas deferens originates from the apex of the prostatic portion of the ovispermiduct, and terminates at the apex of the epiphallus. At this point a strand of connective tissue connects the vas deferens to the penial sheath. The epiphallus opens into the base of the proximal portion of the penis, where a fairly long flagellum originates. The penial retractor is inserted at the apex of the flagellum. The proximal portion of the penis is fairly wide and not demarcated from the distal portion by constrictions. The latter is more slender, surrounded by the penial sheath, and terminates in the genital atrium to one side of the vagina. The inner walls of the penis (Fig. 1A<sub>1</sub> and B<sub>1</sub>) show a plicate structure. The plicae, 5–6 in number, are wavy, sometimes branched and here and there partly interrupted. The opening of the epiphallus is surrounded on both sides by partly fused papillae.

The radula (Plate 3 A and A<sub>1</sub>) consists of numerous rows of teeth each constituted according to the following formula:

$$\frac{8-9 \text{ M}}{1} + \frac{1 \text{ LM}}{2} + \frac{2 \text{ L}}{2} + \frac{\text{C}}{3} + \frac{2 \text{ L}}{2} + \frac{1 \text{ LM}}{2} + \frac{8-9 \text{ M}}{1}$$

The central (rachidial) tooth of each row is formed by a wide plate, providing the base for a short and wide body, from which a pointed mesocone and two shorter ectocones rise. On each side of the central tooth there are two large tricuspid teeth, one latero-marginal bicuspid tooth and 8–9 marginal monocuspid teeth in descending order of size.

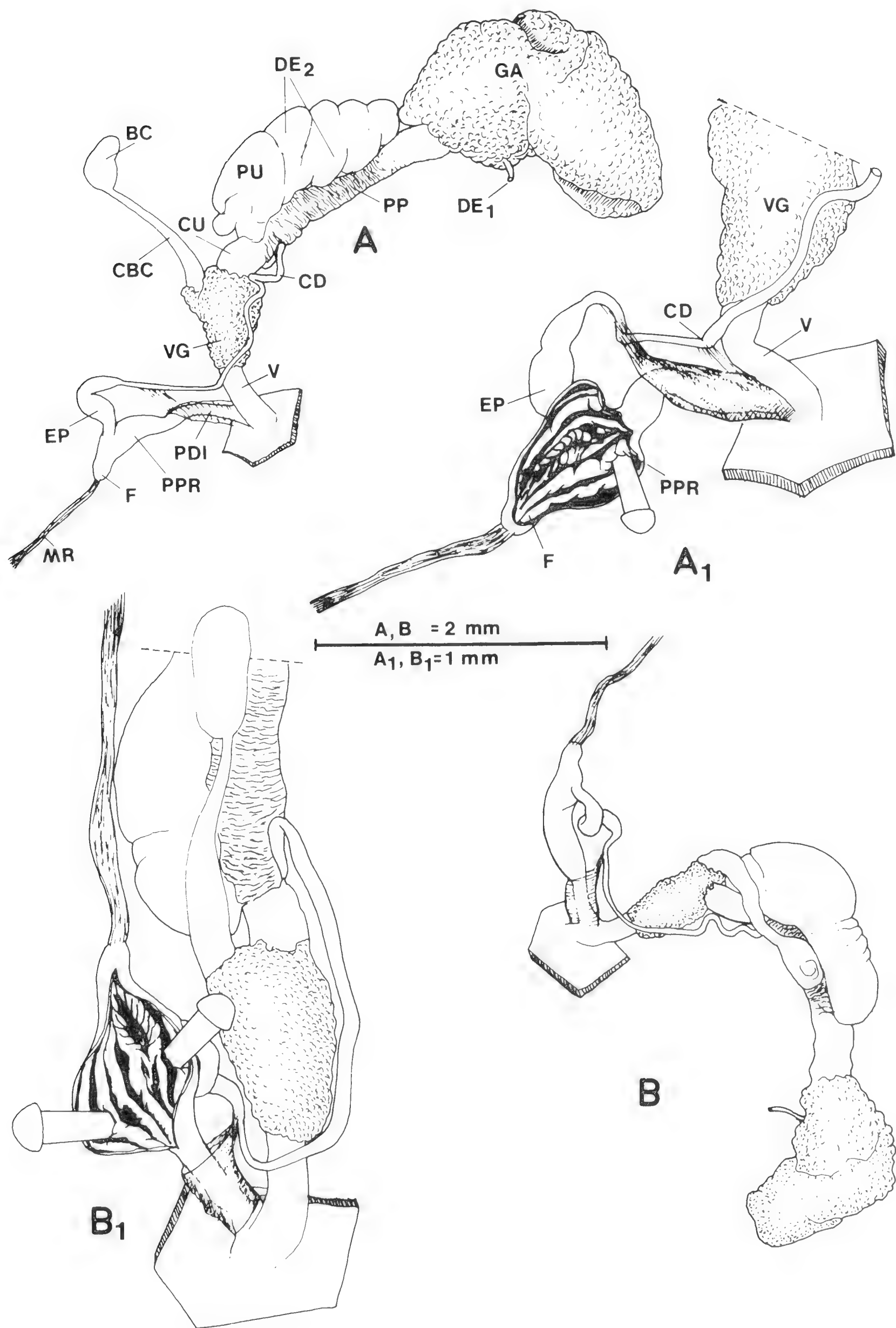


Fig. 1. Genital duct (A and B) and inner structure of the penis (A<sub>1</sub> and B<sub>1</sub>) of two specimens of *O. (Ortizius?) clarus* (Held), collected near Bocognano, Corsica (F. Giusti & G. Manganelli leg. 2 Dec. 1983).

BC bursa copulatrix (=gametolytic gland); CBC duct of the bursa copulatrix; CD vas deferens; CU uterine duct (=free oviduct); DE<sub>1</sub> first hermaphrodite duct; DE<sub>2</sub> second hermaphrodite duct (=ovispermiduct); EP epiphallus; F flagellum; GA albumen gland; VG vaginal gland; MR penial retractor; PDI distal portion of the penis; PP prostatic portion of the ovispermiduct; PPR proximal portion of the penis; PU uterine portion of the ovispermiduct; V vagina.



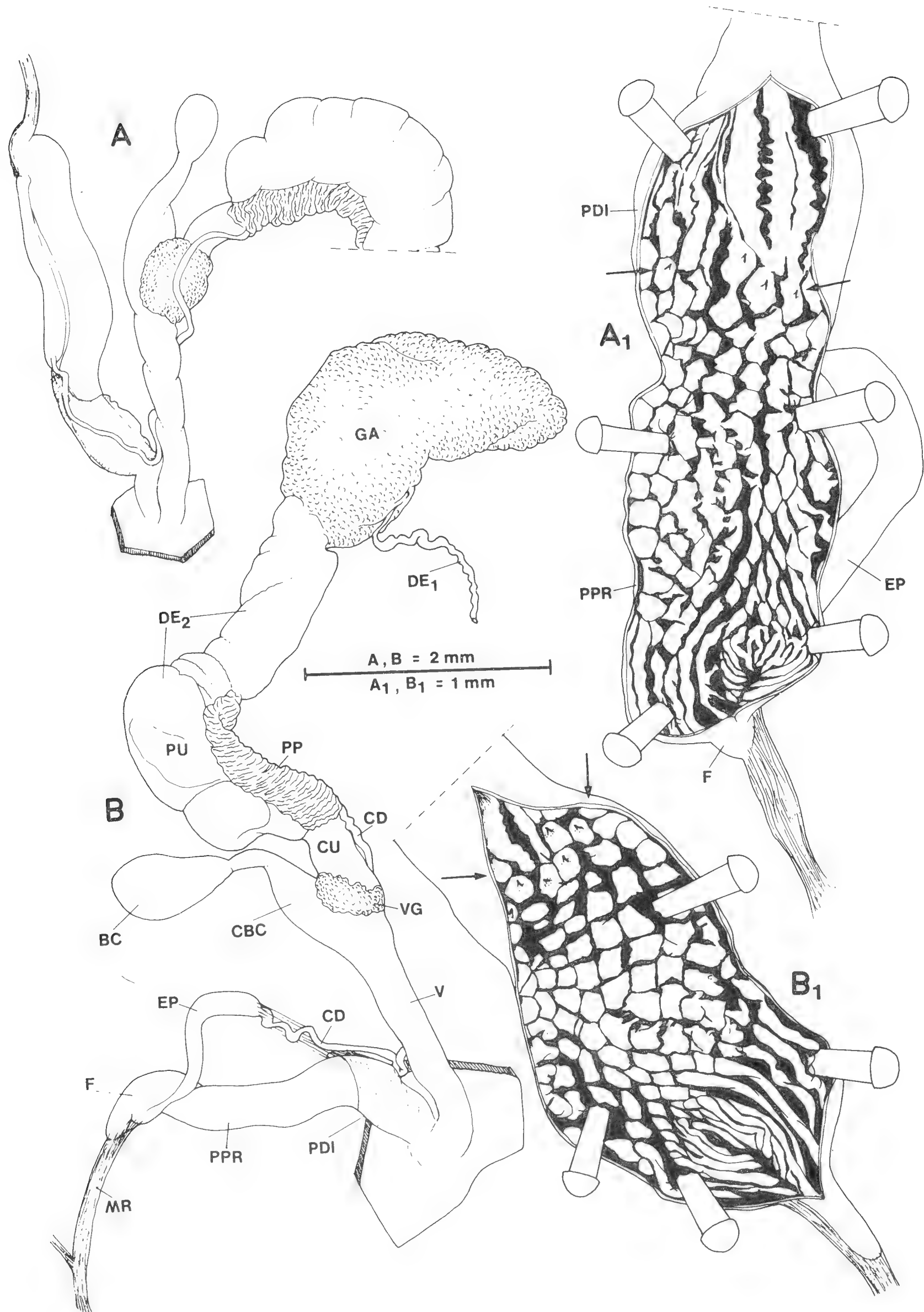


Fig. 2. Genital duct (A and B) and inner structure of the penis (A<sub>1</sub> and B<sub>1</sub>) of *O. (Mediterranea) hydatinus* (Rossmässler) collected near Aleria, Corsica (F. Giusti leg. 30 Nov. 1983). Note the small 'thorns' which are present at the tip of some of the largest papillae in the middle portion of the inner wall of the penis. Abbreviations as in Fig. 1.

*Material examined* (see Fig. 3)

Corsica: 1) Bocognano (600 m), D. T. Holyoak leg. 17 Apr. 1977, 5 shells; 2) Forêt de Vizzavona (900 m), 11 Km NE. Bocognano, D. T. Holyoak leg. 16 Apr. 1977, 1 shell; 3) Debris of the Orbo river near Ghisonaccia, G. Manganelli leg. 30 Nov. 1983, 1 shell; 4) Bocognano (600 m), F. Giusti & G. Manganelli leg. 2 Dec. 1983, 11 shells and 2 living specimens. Alps: 1) France, Dép. Var, Forêt de la Saint-Baume, 700–800 m, 24 May 1948, L. Forcart leg. (Naturhistorisches Museum Basel, no. 5044 c) (shells, spirit specimens and microscope slide); 2) Switzerland, zwischen Samnau und Val-Musauna, 1850–1950 m, 23 June 1945, L. Forcart leg. (NHMB, no. 5044 a) (shells); 3) Switzerland, Fuorca Zeblas, 3500 m, 25 June 1947, L. Forcart leg. (NHMB, no. 5044 b) (shells).

*Habitat*

In Corsica *Oxychilus clarus* appears to live only at relatively high altitudes (600–1000 m) in the litter of woodland of *Castanea sativa* (Bocognano) and *Fagus sylvatica* and *Pinus nigra* (Forêt de Vizzavona), on non-calcareous soils. In the other parts of its range (Alps, Pyrenees and southern France) it appears to also live on calcareous soils, in the litter of woods or on grassy slopes from 400 to 2500 m elevation.

COMPARISONS WITH *O. HYDATINUS* AND *O. PERSPECTIVUS*

The small Corsican *Oxychilus* can be determined as *O. clarus*. This is evident from comparisons with Swiss and French specimens kindly sent by Dr. Forcart of Basel and also from comparisons between the drawings and photos published here and those in the literature (Forcart 1957; Kerney, Cameron & Jungbluth 1983). As anticipated above *O. (Ortizius?) clarus* (Held) is rather similar to *O. (Mediterranea) hydatinus* (Rossmässler) and *O. (Ortizius?) perspectivus* (Kobelt) so summarised descriptions of these are given here, along with taxonomic comments.

*Oxychilus (Mediterranea) hydatinus* (Rossmässler 1838)

Shell (Plate 2 A):  $4\frac{1}{2}$ – $5\frac{1}{2}$  narrow closely-coiled whorls; umbilicus deep and very narrow, not enlarged at the last whorl; maximum diameter 5–7 mm. Body whitish and provided with a small 'Schalenlappen' (=mantle lobe). Genital duct (Fig. 2A–B) with very enlarged base of duct of bursa copulatrix; vaginal gland usually reduced and incomplete; penial retractor extended on one side of the flagellum to reach the base of the epiphallus; penis and flagellum wide and as long as vagina+ovispermiduct; inner walls of penis with many rows of polygonal papillae some of those in the medial portion of the penis being provided with very small 'thorns' (Fig. 2A<sub>1</sub> and B<sub>1</sub>). Radula (Plate 3 B and B<sub>1</sub>) formula: C/3+2L/3+1L–M/2+11–12M/1, with a very small rachidial tooth.

These characters clearly differ from those of *O. (Ortizius?) clarus* (Held) and allow us to restore Rossmässler's species as the type of a separate subgenus: *Mediterranea* (Clessin 1880). *Mediterranea* should include the subgenus *Riedelius* (Hudec 1961) because its type species *O. inopinatus* (Uličný) appears to be a local form of *O. (Mediterranea) hydatinus* (Rossmässler) or a very closely related species (see Riedel 1959, pp. 179–183, Figs. 1–3; 1968, Figs. 3, 8, 9; Pinter 1969, Figs. 7–9). Further research is necessary to establish the affinities of the other species that are currently placed in *Riedelius* (see Riedel 1969, 1980).



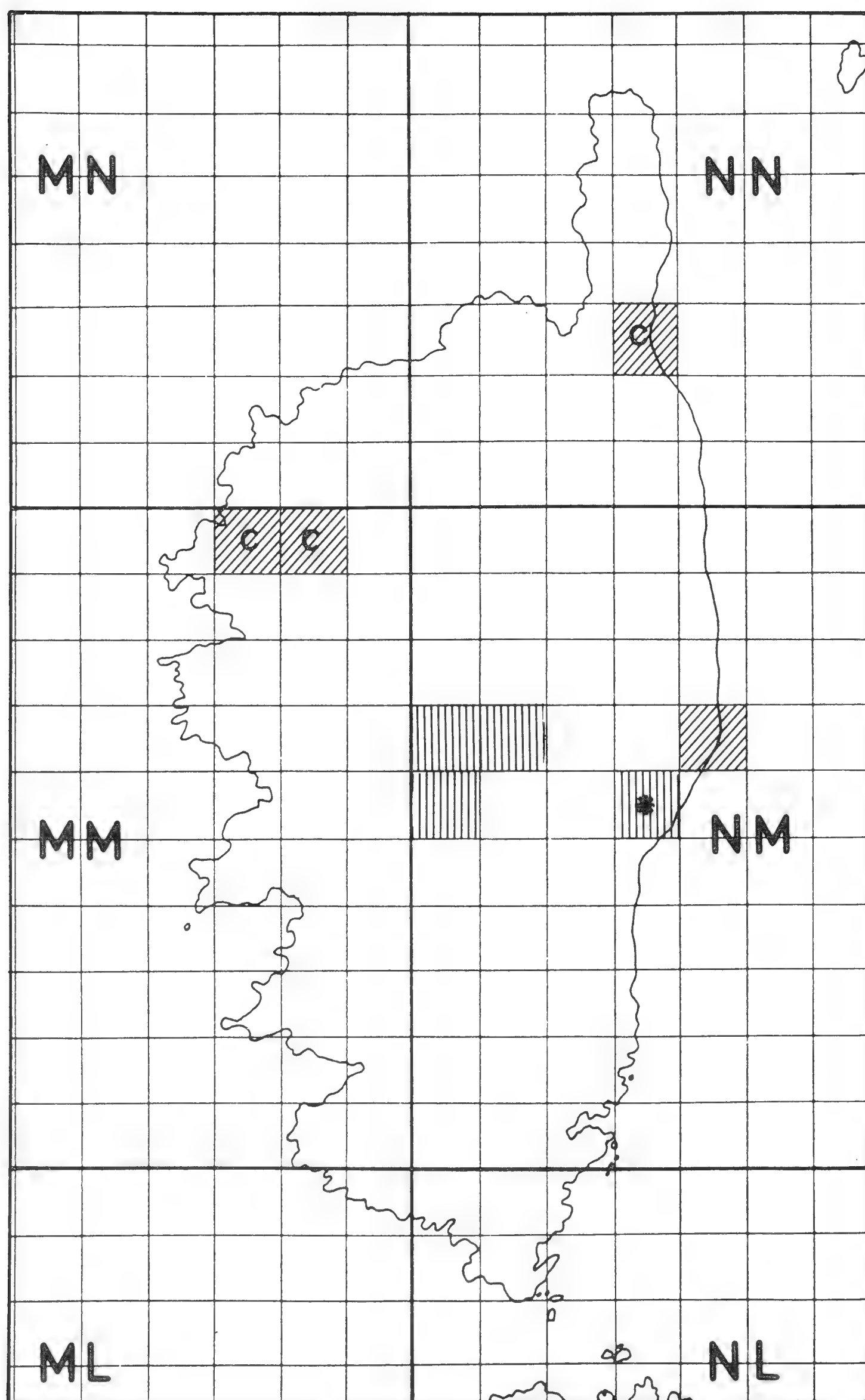


Fig. 3. Distribution of *O. (Ortizius?) clarus* (Held) (vertical lines) and of *O. (Mediterranea) hydatinus* (Rossmässler) (transverse lines) in Corsica. Squares with 'C' come from Caziot's data. The asterisk shows the occurrence of shell material in the debris of the Orbo river near Ghisonaccia.

*Oxychilus (Ortizius?) perspectivus* (Kobelt 1881)

Shell (Plate 1 C, Plate 2 B): 4–4½ rather rapidly expanding whorls; umbilicus broad (c.  $\frac{1}{3}$ – $\frac{1}{4}$  of maximum diameter); last whorl expanded; maximum diameter 6–8.5 mm. Body: whitish, mantle lobe absent. Genital duct: moderately enlarged base of duct of bursa copulatrix; vaginal gland completely enveloping one half of the vaginal duct; apical insertion of penial retractor; penis and flagellum slender and as long as vagina+ovispermiduct; middle portion of the penis narrowed; inner walls of the penis provided with 8–10 longitudinal plicae; no papillae surrounding the epiphallus opening (see Giusti 1973, p. 169, f. 11). Radula: formula C/3+2L/3+1L–M/2+9–11M/1, with very small rachidial tooth (see Giusti 1973, t. 8, f. 5–8). These characters are typical for species which are usually considered to belong to subgenus *Ortizius* Forcart (1957).

The question mark which follows the subgeneric name indicates our doubts about the status of *Ortizius*, which arise because of the existence of many species which show an inner sculpture of the penis which is intermediate between *Oxychilus* (s. str.) and *Ortizius* (Manganelli & Giusti 1984). The closely similar radular formulae and the identical shape of the rachidial tooth of *O. (Ortizius?) clarus* and *O. (Ortizius?) perspectivus* seem less important; their presence also in *O. (Mediterranea) hydatinus* suggests convergence or parallelism.

#### ZOOGEOGRAPHY

The presence of *O. clarus* in natural forest habitats on Corsica is of zoogeographical interest. Corsica and Sardinia were formerly joined to the coast of southern France so that geologically the northern part of Corsica is a fragment of the western Alps (Giusti 1974, 1976, 1977; Giusti & Castagnolo 1984; Giusti & Manganelli 1984). There is a clear affinity between the land mollusc faunas of southern France and Corsica (as well as between those of the Pyrenees and southern France and Sardinia). Thus *O. clarus* may have belonged to the malacofauna of the south-western flank of Europe in pre-Miocene times, before the separation of Corsica and Sardinia from the mainland. However, in the absence of fossil records it is not possible to establish that *O. clarus* has existed since before the Miocene nor to exclude firmly that its presence on Corsica is due to more recent overseas colonisation.

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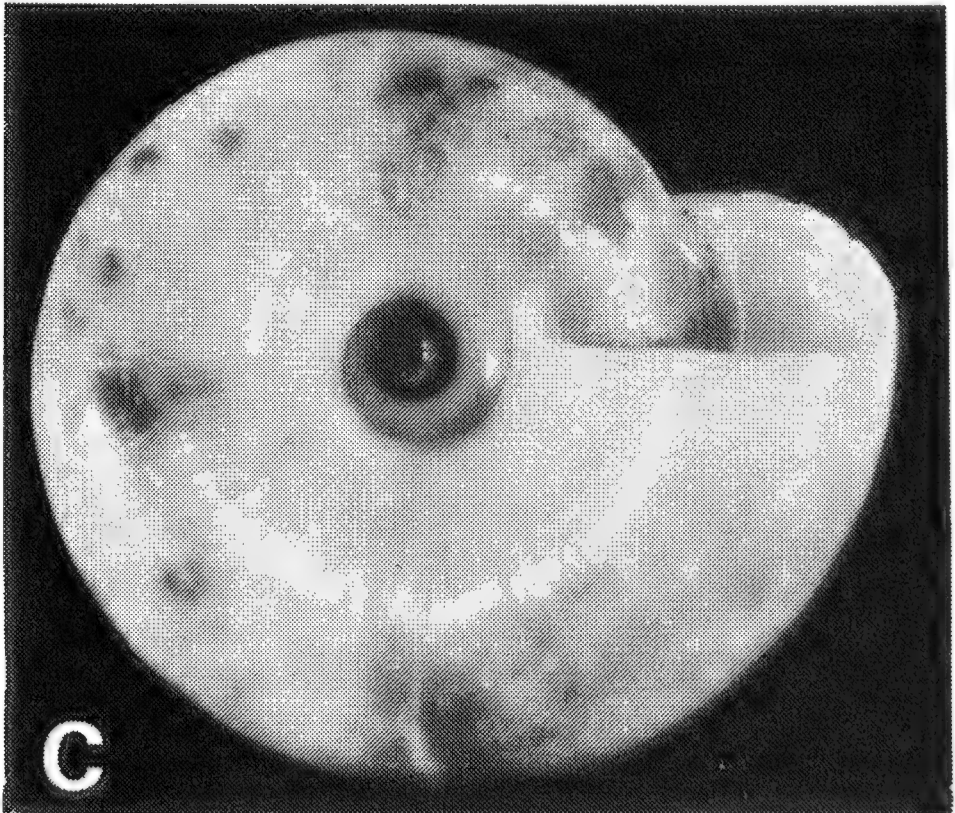
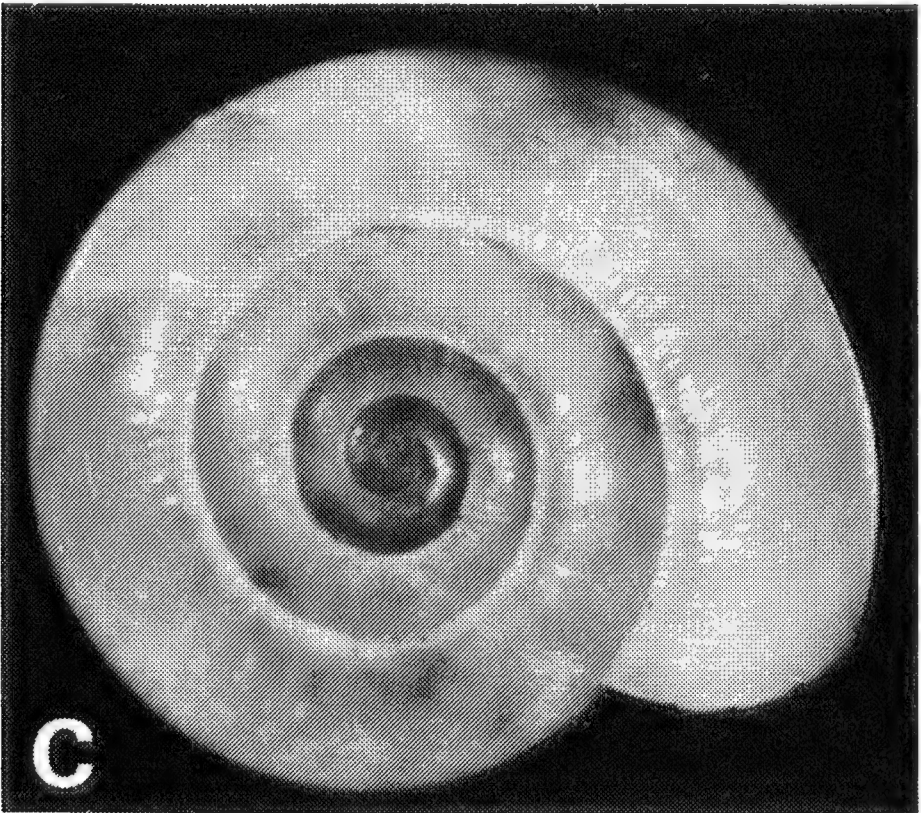
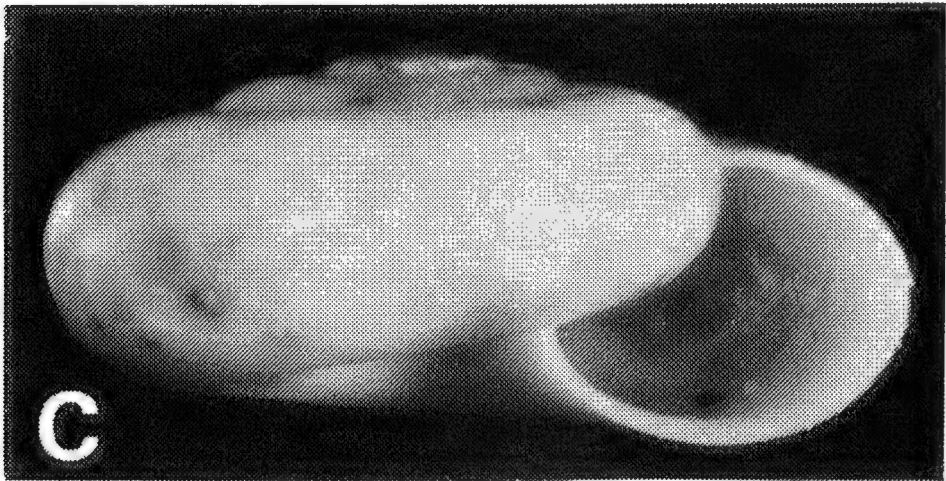
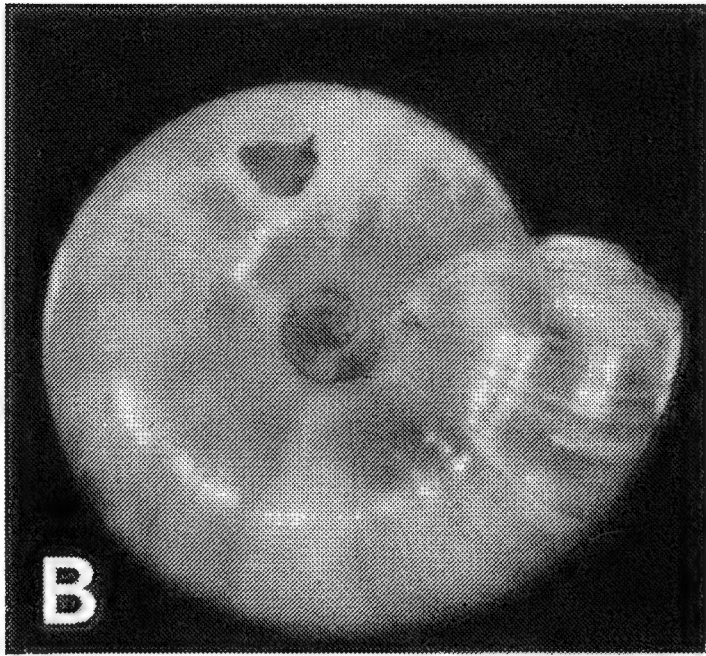
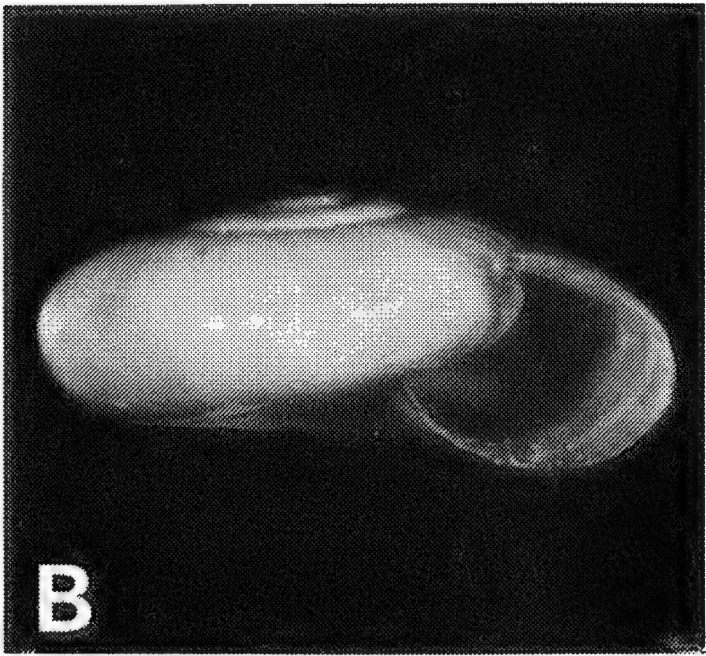
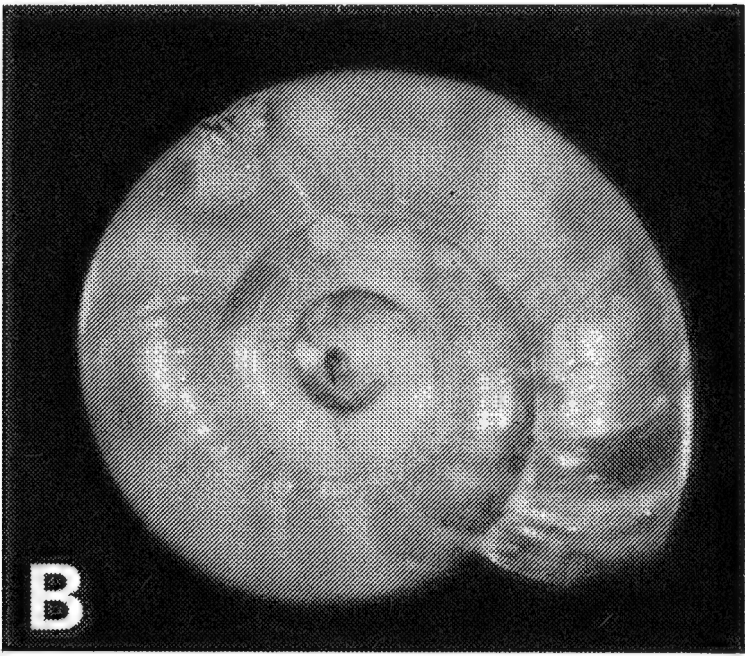
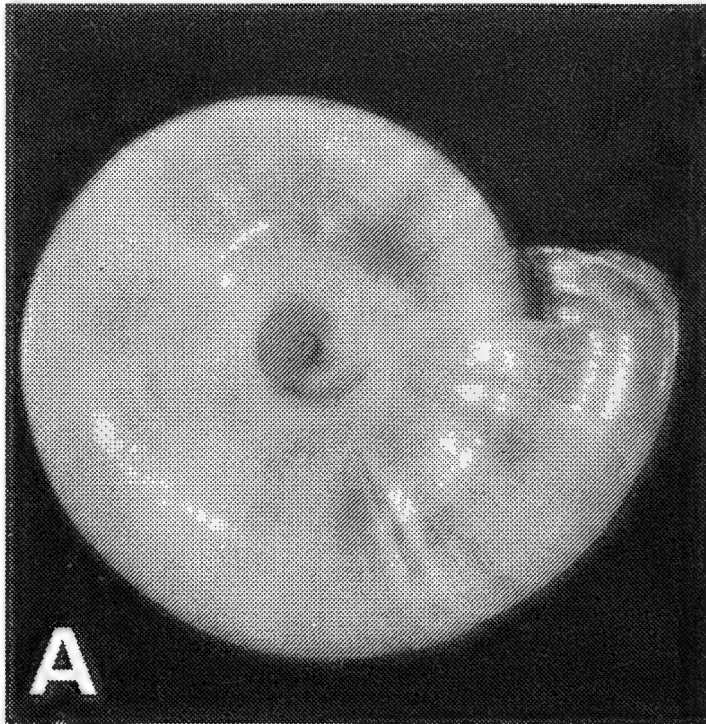
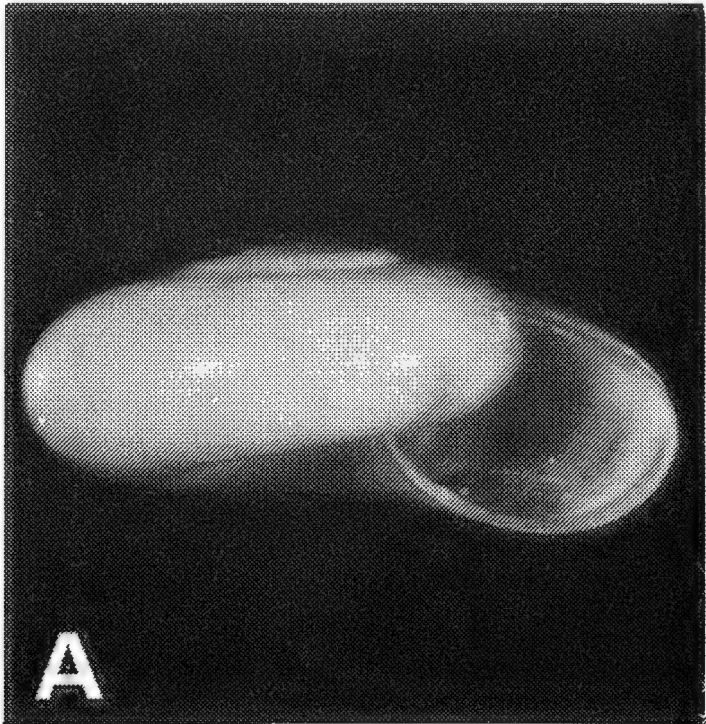
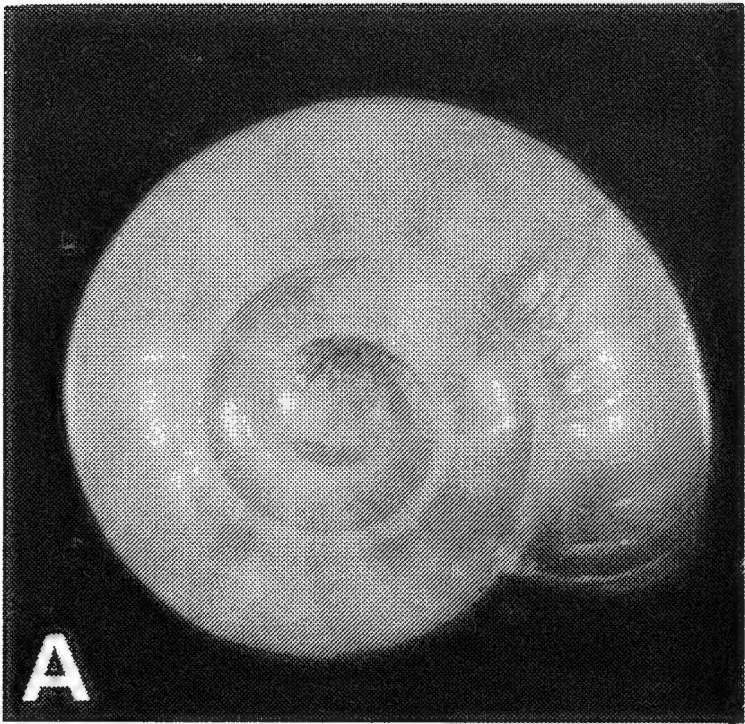
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PLATE 1

A, B, Shells of *O. (Ortizius?) clarus* (Held) Corsica: Bocognano, F. Giusti & G. Manganelli leg. 2 Dec. 1983. C, A small specimen of *O. (Ortizius?) perspectivus* (Kobelt) Eolie Archipelago: Island of Basiluzzo, F. Giusti leg. 15 Nov. 1969.







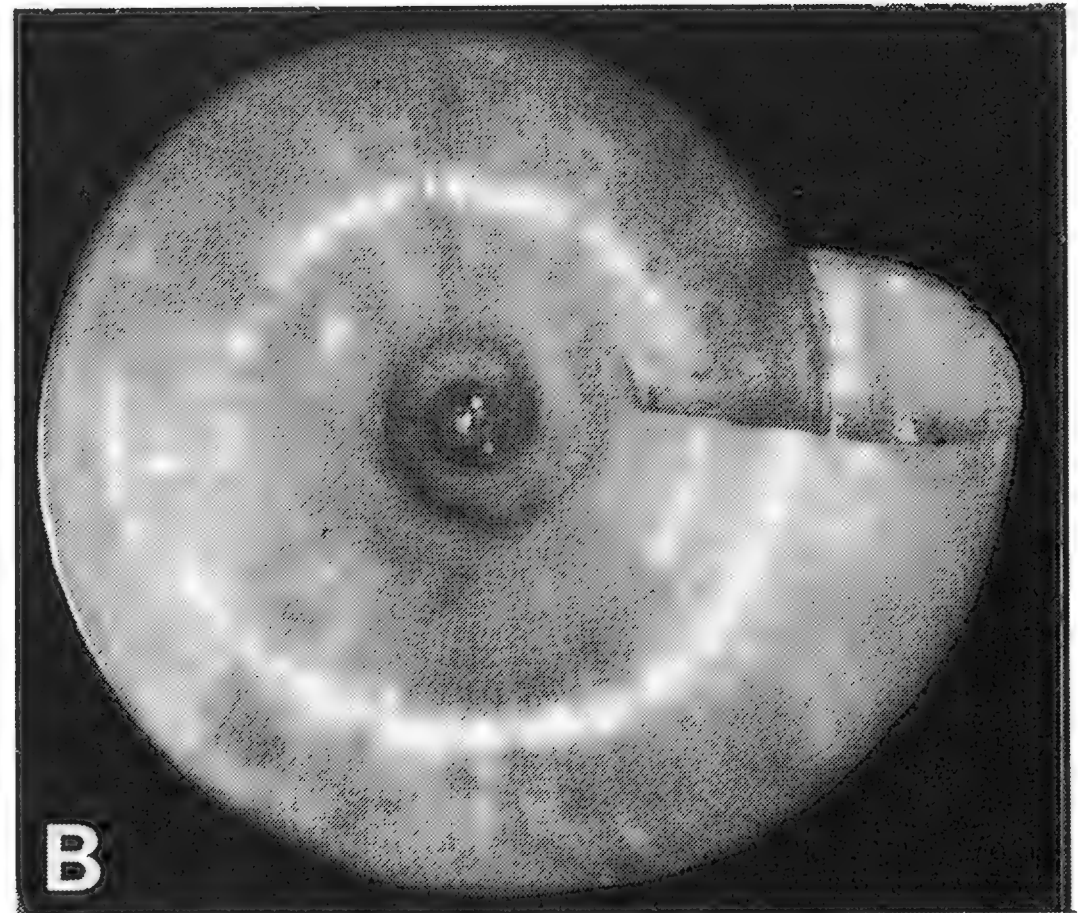
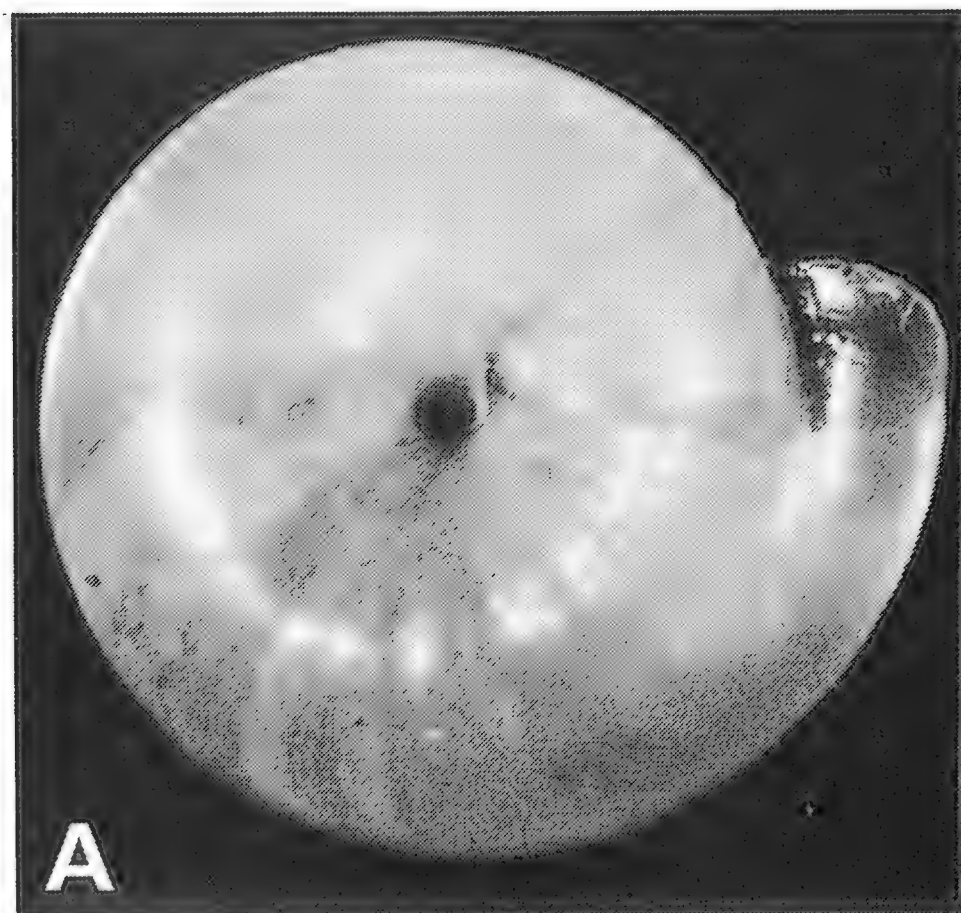
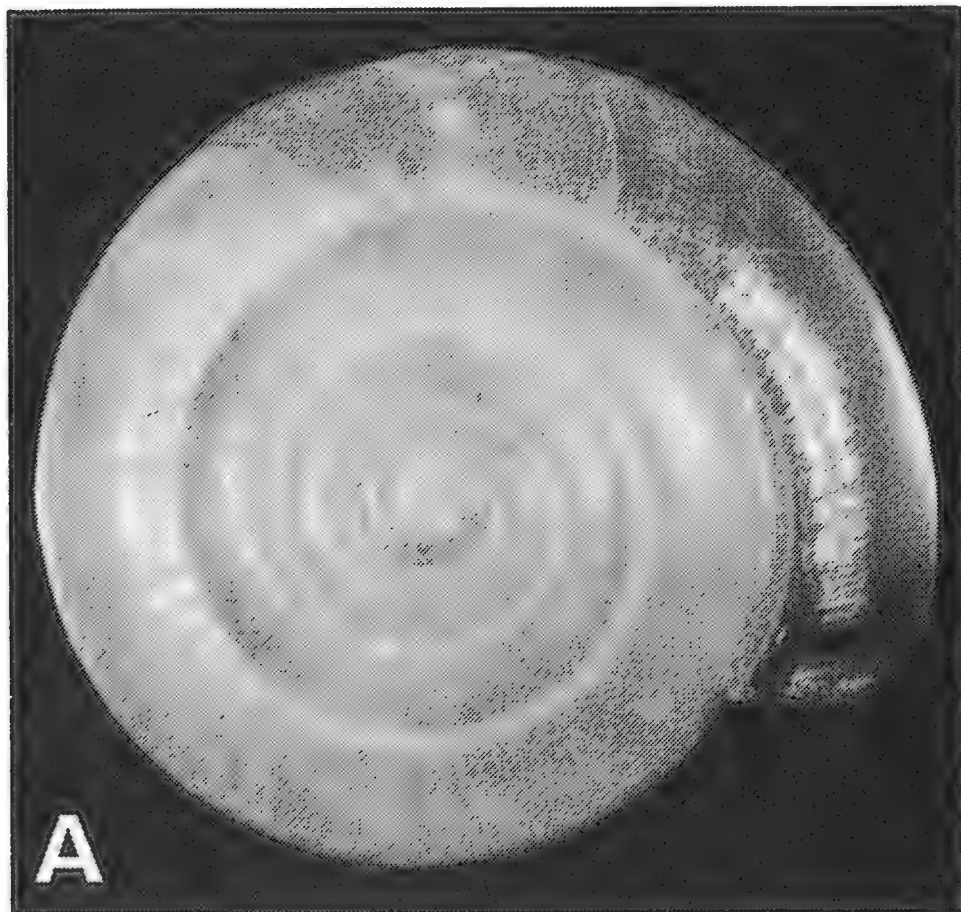
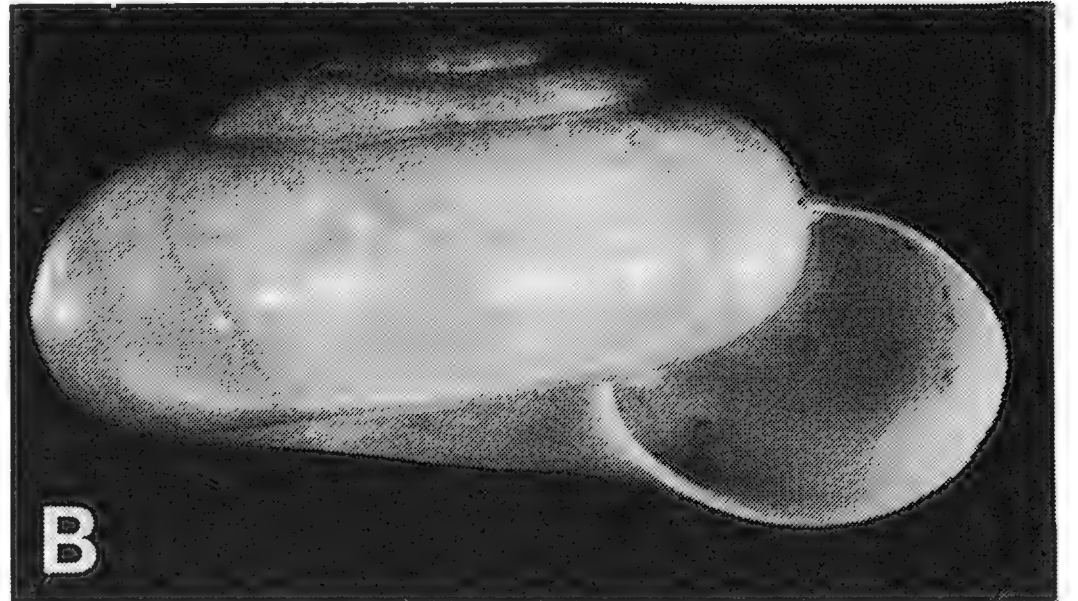
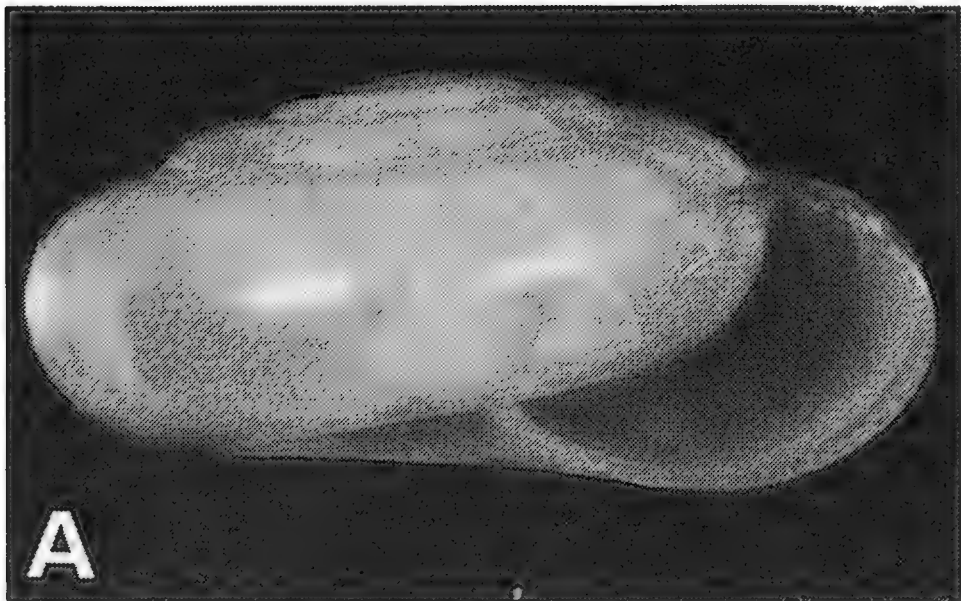


PLATE 2

A, Shell of *O. (Mediterranea) hydatinus* (Rossmässler) Corsica: Aleria, F. Giusti leg, 30 Nov. 1983. B, A large specimen of *O. (Ortizius?) perspectivus* (Kobelt) Eolie Archipelago: Island of Stromboli, F. Giusti leg. 16 Apr. 1968.



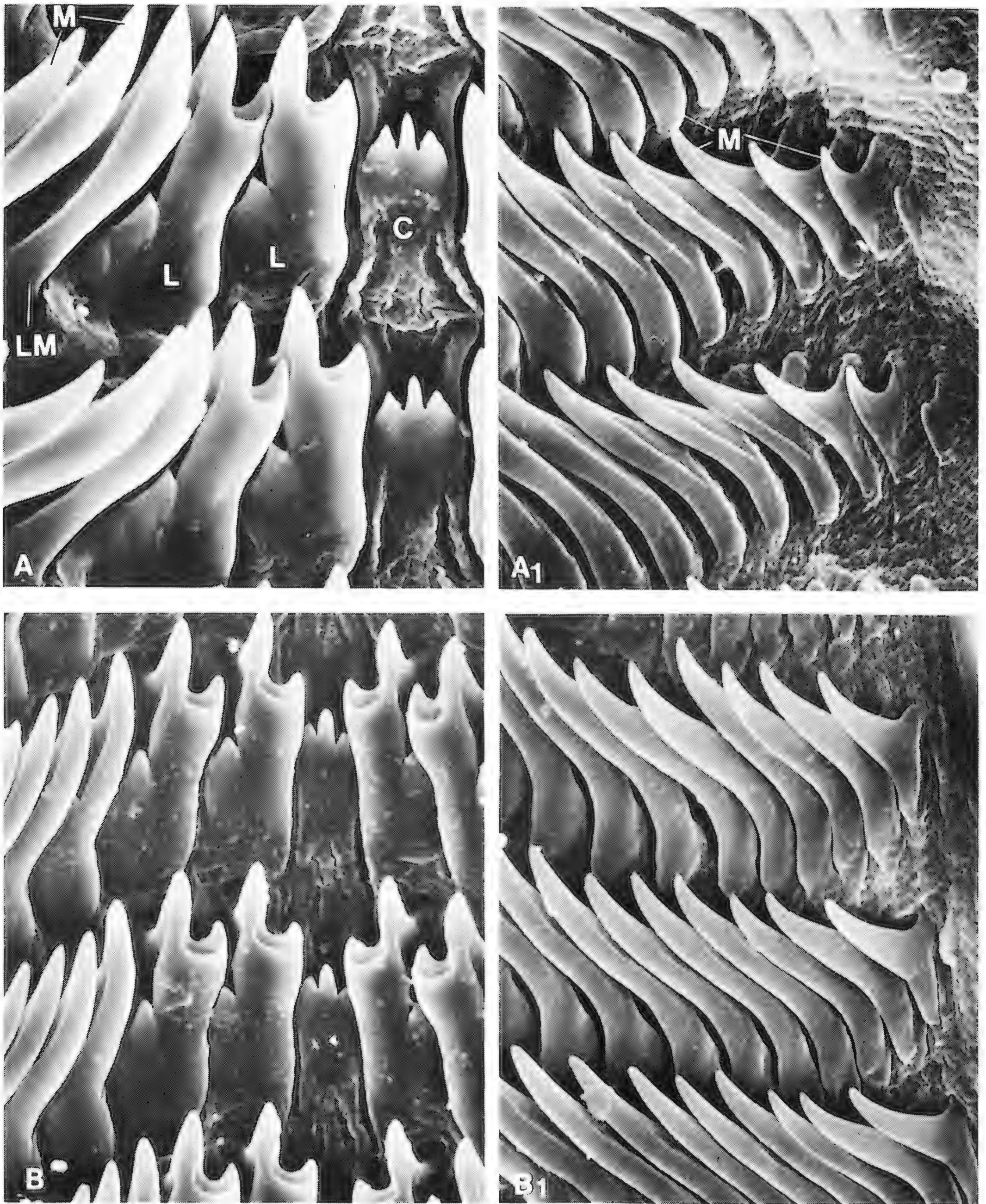


PLATE 3

A, A<sub>1</sub>, Portion of the radula of *O. (Ortizius?) clarus* (Held). B, B<sub>1</sub>, Portion of radula of *O. (Mediterranea) hydatinus* (Rossmässler) (B-B<sub>1</sub>). C central tooth; L lateral teeth; LM latero-marginal tooth; M marginal teeth; A×1000; A<sub>1</sub>×800; B and B<sub>1</sub>×600.





# THREE NEW BUCCINIDS FROM OMAN AND NOTES ON *ANACHIS FAUROT* (JOUSSEAUME) (PROSOBRANCHIA: BUCCINACEA).

KATHLEEN R. SMYTHE<sup>1</sup>

(Accepted for publication, 20 October 1984)

*Abstract:* This paper describes and illustrates three new species from Oman, *Anachis raysutana*, *Costoanachis rassierensis* and *Latirus bonnieae*, and illustrates the lectotype, protoconch, operculum and radula of *Anachis fauroti* (Jousseaume 1888). The first three are from areas associated with the upwellings in the North Arabian Sea and affected by the south-west monsoon and the last named has a wider distribution from the Gulf of Aden to the Mekran coast and within the Arabian Gulf. *Latirus bonnieae* is the only species in this paper of which the animal and radula are unknown.

## INTRODUCTION

For several years the correct identity of several species of *Columbellidae* from Arabia and a species of *Latirus* from Oman has been puzzling me.

After extensive study of the literature on the Erythraean, Arabian, Iranian and Pakistani regions in particular and of the Indo-Pacific in general, and examination of the large collections from these areas in the British Museum (Natural History) [BMNH] and the National Museum of Wales, Cardiff [NMW] and in private hands, I have come to the conclusion that three of the species now under discussion are to date undescribed and one has figured in the literature under the wrong name. Therefore I now propose to describe two *Columbellids* and one *Latirus* from Oman, and to make some comments on *Anachis fauroti* (Jousseaume) from the North Arabian Sea and its adjoining Gulfs.

For colour names I have used Rayner (1970) as this work provides a definite name and number for various colours and can be applied in more aspects than its original purpose for the use of malacologists.

In assigning the *Columbellids* to their genera I have followed Radwin (1977 & 1978) and consulted Pace (1902) as well as standard general works.

I have not gone into details about the anatomy of the *columbellids* as this is typically *buccinid* and very similar (though reversed of course) to that of *Sinistralia gallagheri* (Chatfield & Smythe 1982). The tentacles are moderately short and slender and have eyes at the base of them. The gill is conspicuous through the thin mantle covering; the penis in males is large.

The anatomy of *Latirus bonnieae* is not known. When the Holotype was found, it was not realised that the soft parts were still inside the shell, so unfortunately only the operculum was recovered from the decomposing matter.

<sup>1</sup> 6, Blondell Drive, Bognor Regis, West Sussex, PO21 4BQ.

Family: Columbellidae

Subfamily: Pyreninae

Genus: *Anachis* H & A Adams 1853

*Anachis fauroti* (Jousseaume 1888)

*Atilia fauroti* Jousseaume 1888, p. 177

*Columbella* (*Mitrella*) *zebra* Gray (Melvill & Standen 1901, p. 404).

*Columbella miser* Sowerby (Shopland 1902, p. 173).

*Columbella* (*Mitrella*) *zebra* Gray (Melvill 1903, p. 30).

? *Columbella* (*Anachis*) *terpsichore* Sowerby (Sturany 1903, p. 40, Tafel V, Figs. 4a & b).

*Mitrella* (*Mitrella*) *misera* (Sowerby) (Biggs 1973, p. 368).

*Mitrella misera* (Sowerby) (Smythe 1979, p. 67 & 75.)

*Anachis misera* (Sowerby) (Bosch & Bosch 1982, p. 98).

### *Material examined*

Four syntypes of *Atilia fauroti* in the Muséum National d'Histoire Naturelle, Paris, [MNHN] from which is selected a lectotype (Plate 4, Fig a): the Melvill collection in the National Museum of Wales [NMW] which contains the shells referred to by Melvill & Standen (1901) and Melvill (1903): the Commander Shopland collection from Aden, donated by him in 1907 to the Royal Albert Memorial Museum, Exeter: my own collection and those of friends and my recollections of the material examined by the late H. E. J. Biggs..

### *Summary of diagnostic features*

A small, elongated oval shell, with rounded axial ribs, a narrow aperture with the outer lip thickened and toothed within, white patterned with black wavy streaks and blotches.

### *Description*

Little, apart from details of operculum, radula and protoconch of live molluscs collected from Masirah, Oman, can be added to Dr. Jousseaume's excellent description, but for the sake of those without easy access to his paper I incorporate some of his words with my own. *Shell*: an elongated oval with a pointed apex, solid and heavy. The protoconch (Fig. 2) has  $1\frac{1}{2}$  smooth translucent whorls; axial ribs commence on the third whorl which also has the first indications of the dark patterning. Subsequent whorls are sculptured with rounded, regular axial ribs separated by narrow interspaces, both ribs and interspaces being crossed by very fine spiral striae. The sutures are lightly impressed and wavy, due to the ribs impinging on the previous whorls. The body whorl is constricted at the neck, the ribs giving place to spiral cords. There are 14 to 15 ribs on the body whorl.

*Aperture*: long and narrow with the outer lip thickened in the centre and with a few small denticles inside the aperture. The columella is straight with a few weak plications and a slight callus. The siphonal canal is short, narrow and inclined to the left.

*Colouring*: the pattern is a dull black on a white ground, the black showing on the ribs as elongated wavy blotches and irregular streaks; dark blotches sometimes occur also on the columella and within the aperture which are otherwise white.



*Periostracum*: pale amber (Rayner: no. 47), coarse with longitudinal (axial) fibres, often eroded, especially on the apical whorls and the ribs.

*Size*: a random sample of ten shells from Rassier, Masirah, was measured. The body whorl is approximately 66% of the height and the aperture 50% of the height. The average height of shell was 14.28 mm, diameter 5.99 mm, body whorl height 9.60 mm and aperture length 6.75 mm. The largest shell was 16.25 mm in height, the narrowest 16.25×6.20 mm, the broadest 12.00×5.00 mm.

*Animal*: the underside of the foot is white. The upper part of the animal and mantle are white profusely spotted and blotched with black, as is the siphon.

*Radula* (Fig. 8): very long and narrow in the form of a tube. The cusplless central teeth are wide and slender and fairly close to each other on the radular membrane. The laterals have three cusps and a blunt process attaching the tooth to the membrane. All the lateral teeth in the species discussed in this paper are somewhat twisted as well as being curved to conform with the tubular shape of the radula. Radwin states that they are sigmoid, but this does not seem to me to exactly convey the distortion of the teeth.

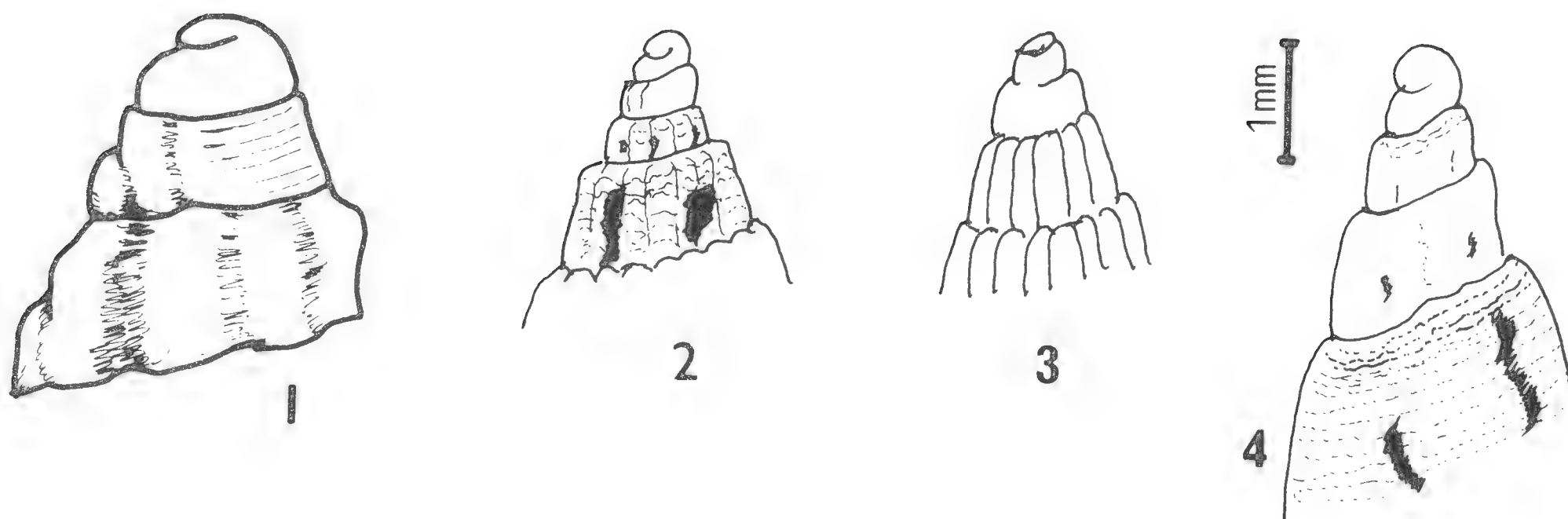
*Operculum* (Fig. 5): lanceolate with an apical nucleus, often broken. It is horny, moderately solid, dark brown. Growth striae mark the dull exterior. The muscle scar is dull and lanceolate with a ridge around it and the varnish layer surrounding this is highly glazed.

*Habitat*: these molluscs appear to live singly, but usually with several other individuals nearby, on or under small stones or rocks on a reef or on fine sand or silt, but I have not found them living in sand or silt as does *Mitrella blanda* (Sowerby). They can be found in the intertidal area, usually nearer the low tide mark, occurring on both hard and soft rock.

*Known distribution*: Obock (Jousseaume): Oman—general (Bosch & Bosch 1982): Linja (Iran) and the Mekran Coast (Melvill & Standen 1901, Melvill 1903): Hilat al Bahrani (Abu Dhabi) and Aden (Biggs 1973): As Shaam, Khor Hulaylah, Umm al Qawain and Sharjah (United Arab Emirates) (Smythe 1979): Tahiri (Iran) KRS collection leg. Mrs. J. Ainsworth, Nursing Sister, now of Chichester, Sussex: Hormuz Island, KRS collection and Ferdowsi University, Mashhad, collection, leg. KRS: Khor Fakkan and Shaam (United Arab Emirates, Gulf of Oman) KRS collection, leg. KRS and M. D. Gallagher: Raysut and Mirbat, (Dhofar, Oman) Oman Natural History Museum [ONHM], BMNH, KRS collection, leg. KRS, M. D. Gallagher, Dr. J. D. Taylor & Dr. Lynne Barratt: Haql, Kalban, Rassier and Umm Rusays (Masirah Island, Oman) leg. KRS, M. D. Gallagher and Dr. and Mrs. Donald T. Bosch: Sur and Ras al Hadd, leg. KRS & M. D. G.: ?Red Sea (Sturany 1903).

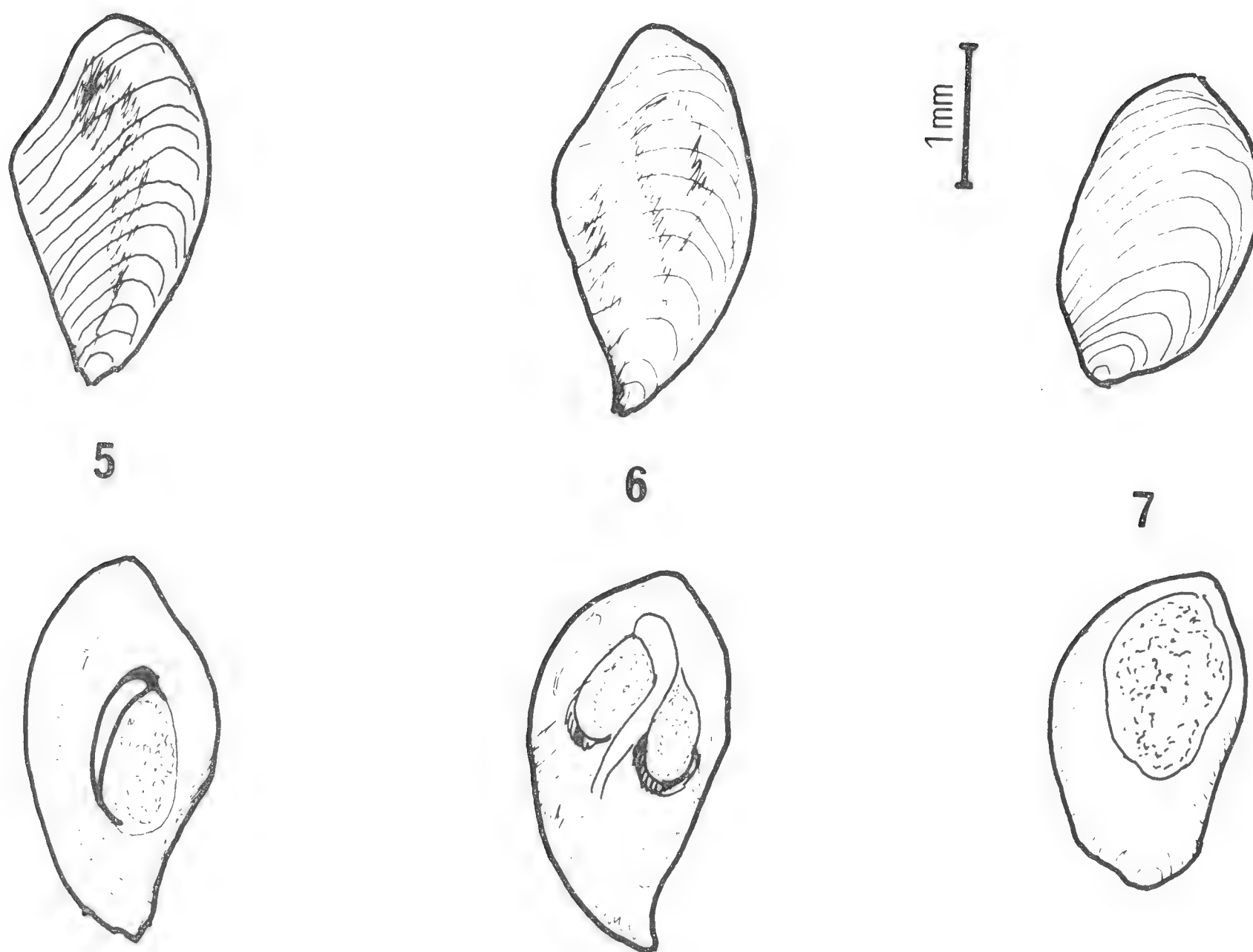
### Comment

It has become evident that the shells from the Arabian and Iranian coasts called variously *C. miser*, *C. zebra* and *M. misera* by the authors mentioned in the synonymy are in fact *A. fauroti* (Jousseaume). Sturany's illustration of the shell he called *C. terpsichore* Sowerby is excellent and appears to be *A. fauroti* rather than *C. terpsichore* which Sowerby figured as a shell with nodules at each end of the axial ribs; these nodules are evident in shells in various collections as well as in the probable type in BMNH. The exact identity and affinities of *C. zebra* and its allies are not a matter for concern here, as it appears that they do not occur in Arabia and Melvill's identification with subsequent authors following him, was probably based on the poor figures and descriptions of Gray and Sowerby.



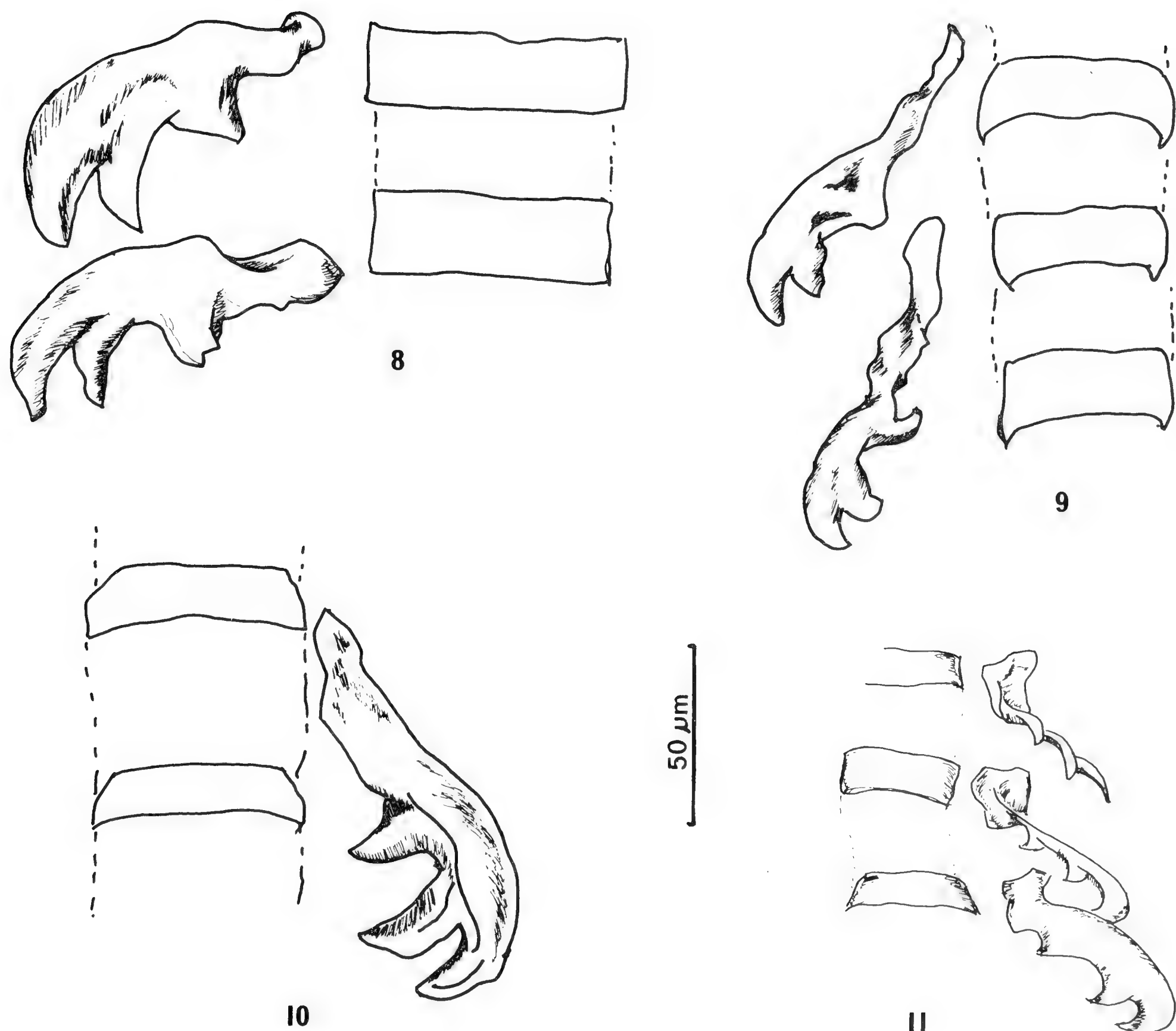
Figs. 1-4 Protoconchs

1. Protoconch of *Latirus bonnieae*: shell height 51.25 mm
2. Protoconch of *Anachis fauroti*: shell height 14.5 mm
3. Protoconch of *Anachis raysutana*: shell height 12.5 mm
4. Protoconch of *Costoanachis rassierensis*: shell height 12.5 mm



Figs. 5-7 Opercula.

5. Operculum of *Anachis fauroti*: shell 12.5 mm
6. Operculum of *Anachis raysutana*: shell 12.5 mm
7. Operculum of *Costoanachis rassierensis*: Shell 10 mm



Figs. 8-11 Radulae.

8. Radula of *Anachis fauroti*

9. Radula of *Anachis raysutana*

10. Radula of *Costoanachis rassierensis*

11. Radula of *C. rassierensis*. to show torsion of the lateral teeth.

Figures 8 to 10 are approximately  $\times 4$  fig. 11.

## DESCRIPTIONS OF NEW SPECIES

Genus *Anachis* H. & A. Adams 1853.

***Anachis raysutana*** sp. nov. (Plate 4 Figs, b & c.)

### *Summary of diagnostic features*

Small, broadly fusiform, axial ribs somewhat angular and widely spaced, aperture elongate with many denticles within, colour white patterned with zigzag markings of brown.



*Description*

*Shell*: fusiform when young, becoming broad at the anterior when adult, fairly light weight compared with the preceeding and following species. Protoconch (Fig. 3)  $2\frac{1}{2}$  glassy whorls, usually eroded, followed by one smooth opaque colourless whorl; subsequent whorls are ribbed. The ribs are somewhat angular, rather than rounded, and are widely spaced, the interspaces being flat and shallow with microscopic axial striae following the lines of growth. The ribs occupy one third of the body whorl, the centre of the whorl being sculptured only by the very fine axial striae and the lower third being encircled by strong, rounded, well-spaced spiral cords crossed by fine striae. There are 9 to 10 ribs on the body whorl. The whorls are angled at the shoulders and the sutures are deeply impressed.

*Aperture*: elongated, outer lip thickened, especially in the centre in adult shells, with up to 10 plications extending from the labrum into the aperture and the siphonal canal. The columella is straight and smooth with a thick callus. The anterior canal is wide and inclined to the left.

*Colouring*: ground colour white, apical whorls pale ivory. The colour pattern commences on the fourth or fifth whorl and consists of 'tent markings' similar to that of the textile cones, and of zigzag streaks and blotches of yellow to reddish-brown (Rayner: pale luteous no. 11, ochreous no. 44, cinnamon no. 62, bay no. 6, sienna no. 8 and umber no. 9).

*Periostracum*: very pale, almost colourless, with fine longitudinal fibres following the lines of the growth striae, often almost completely eroded.

*Size*: a random sample of ten shells from Umm Rusays, Masirah, was measured. The body whorl is approximately 70% of the total height and the aperture nearly 50%. The average height of shell was 12.98 mm, diameter 5.90 mm, body whorl 9.15 mm and aperture length 6.85 mm. The largest shell was 14 mm in height. The narrowest shell 13 mm × 5.75 mm and the broadest 11.50 × 5.75 mm.

*Animal*: uniformly pale café-au-lait colour above and below; some specimens have a few pale brownish blotches on the body.

*Radula* (Fig. 9): very long and narrow in the form of a tube. The cusplless central tooth is widely separated from those next to it. The laterals have three slender cusps and long processes engaging with the connective membrane. They are somewhat curved and twisted.

*Operculum* (Fig. 6): lanceolate with a terminal nucleus, often broken off. Horny, thin, pale brown. The exterior is slightly convex and twisted, dull and marked with growth striae. The muscle scar is dull with a ridge crossing the centre; the varnish layer round the edge is highly glazed.

*Habitat*: The molluscs appear to live singly and not in groups, on or under loose rocks of soft limestone on silty sand or in silty pockets on reefs.

*Etymology*: named for Raysut, Oman, whence the first specimen was sent to me, collected on 29 January 1979 by Mr. M. D. Gallagher [MDG].

*Holotype*: BMNH registered number 1984079. leg. KRS, bay west of Raysut, 16 February 1984, live on flat rocky reef with algae and silt. Height 14.05 mm, width 6.60 mm, aperture length 7.00 mm.

*Paratypes*: BMNH registered number 1984080; ONHM Accession number 1984/69/B; NMW Accession number 1984.047.1 and 047.2. Paratypes are also in BMNH collected by Dr. J. D. Taylor from Raysut in October 1983 and others have been deposited in the Zoölogisch Museum, Amsterdam, the Muséum National d'Histoire Naturelle, Paris, the Smithsonian Institute, Washington, DC, and the American Museum of Natural History, New York. Paratypes are also in the collections of KRS and of Dr. and Mrs. Bosch, of Cambridge, New York.

*Known distribution:* *A. raysutana* has been found near Raysut, Oman (16°56'N, 54°00'E) in 1979 and 1984, leg KRS and MDG and Dr. J. D. Taylor in 1983. Also on Masirah Island at the northern tip (20°41'N, 58°54'E) leg, KRS and MDG January 1982: cast up on the beach north of Rassier, leg. Mr. M. C. Jennings November 1979: Rassier on loose limestone boulders (20°32'N, 58°57'E) and Haql (20°21'N, 58°38'E) leg KRS, December 1980: Ras Shagaaf (20°29'N, 58°48'E) and Umm Rusays (20°27'N, 58°48'E) leg KRS and Dr. D. T. Bosch, January 1984.

#### *Comment*

The shell bears some resemblance to certain colour forms of '*Columbella*' *ligula* Duclos, which also occurs in Oman, not only in colouring and pattern but in the general shape with angled shoulders and deep sutures. However the five syntypes of *C. ligula* in MNHN, Paris, show this to be a smooth species with no trace of ribbing. Also its colour pattern is very variable.

Genus *Costoanachis* Sacco 1890

***Costoanachis rassierensis*** sp. nov. (Plate 4, Figs. d & e)

#### *Summary of diagnostic features*

A small ovoid shell, apex pointed, aperture long, with 3–5 denticles within the outer lip, colour white densely patterned with yellow, brown or black.

#### *Description*

*Shell:* ovoid with a sharp, pointed apex, very thick and heavy (surprisingly so in comparison with the animal which is small). Protoconch (Fig. 4) 1½ glassy, translucent whorls, followed by 2 semi-translucent whorls with a few microscopic punctate spiral striae. The next whorl bears a few spots of colour; subsequent whorls are coloured and have spiral striae or grooves becoming deeper as the shell increases in size. The axial ribs commence either on the body whorl or on the whorls immediately preceding it. The ribs are wide at the suture where they almost touch, becoming narrower anteriorly with the interspaces becoming correspondingly wider. The ribs are smooth and rounded, the interspaces spirally grooved. The anterior third of the body whorl lacks the ribs but is encircled by broad, flat spiral ridges, narrowly grooved between. There are 13–14 ribs on the body whorl. The sutures are impressed but not deep, the whorls are rounded and not angled at the shoulders.

*Aperture:* elongate, the outer lip thickened at the centre but thinner and finely plicate at the anterior. There are 3 to 5 small denticles within the aperture. The columella is straight with up to 5 weak plications; some shells have none. The columellar callus is glossy, white sometimes blotched with colour, sometimes detached a little at the edge. The siphonal canal is short, wide and inclined to the left; it is deeply notched on the dorsal surface of the shell.

*Colouring:* the ground colour is white densely patterned with colour from pale yellow through brown to dark grey or black (Rayner: luteous no. 12, amber no. 47, isabelline no. 65, sepia no. 63, iron grey no. 122 and leaden black no. 126). The shells are uniformly of one colour and white—there is no mixture of colours on one shell. The apical whorls are

white, the subsequent whorls coloured and the ribs are white posteriorly with colour between and overlaid with colour below. The anterior third of the body whorl is mostly suffused or heavily streaked with colour. The majority of shells are of the darker colours but a minority are pale. The outer lip is edged with colour and the aperture is white within, the darker colour of the exterior sometimes showing through inside.

*Periostracum*: Coarse, amber coloured, with axial fibres similar to those of *A. fauroti* but coarser than those of *A. raysutana*, usually eroded on the apex and ribs.

*Size*: a random sample of ten shells from Ras al Jazirah near Rassier was measured. The body whorl is approximately 75% the height and the aperture 50% the height. The average height of the shells was 11.72 mm, diameter 4.92 mm, body whorl height 8.16 mm and aperture length 5.73 mm. The largest shell was 13.5 mm. The narrowest was 13.5×5.4 mm, the broadest 12.25×5.5 mm.

*Animal*: the underside of the foot is white, the upper part of the animal and the mantle white, lightly spotted with black. The siphon has a white tip with a black band below.

*Radula* (Figs. 11, 12): very long and narrow, tubiform. The uncusped central plates are widely rectangular, the corners a little angled off, and well separated from each other. The laterals have three rather broad, sharp cusps and the processes engaging with the connective membrane are blunt. The teeth are slightly curved and twisted.

*Operculum* (Fig. 7): a rounded oval, thin, horny, light reddish-brown. The slightly convex exterior is dull, with concentric striae radiating from a terminal nucleus. The interior has a dull, irregularly shaped muscle scar surrounded by a glossy varnish layer.

*Habitat*: the molluscs live in dense colonies of up to a hundred individuals, apparently towards the upper part of the intertidal zone, on cliffs or rocks or in crevices. There may of course be a seasonal migration down the shore. They seem to inhabit areas where the rock is hard (granite in Dhofar, peridotite on Masirah) rather than the softer limestones.

*Etymology*: named for Rassier, Masirah, where I first found living specimens.

*Holotype*: BMNH registered number 1984082, leg KRS, Ras Dha, Masirah, 18 January 1984, live on low cliff. Height 12.2 mm, breadth, 5.35 mm, aperture 4.40 mm

*Paratypes*: BMNH registered number 1984083; ONHM Accession number 1984/69/C; NMW Accession number 1984.048.1 and 048.2. Paratypes are also in BMNH, collected by Dr. J. D. Taylor in October 1983 from Mirbat and in all the collections named for *A. raysutana*.

*Known distribution*: Masirah Island, Oman, from Ras Dha (20°26'N, 58°44'E), Ras al Jazirah (20°35'N, 58°48'E), Rassier (20°32'N, 58°57'E): Southern Province (Dhofar), Oman, from Mirbat (16°58'N 54°42'E) to Khawr Maratma (17°03'N, 55°05'E). All leg. KRS and MDG; some leg. Dr. Taylor (Mirbat) and some Dr. D. T. Bosch (Masirah, probably east coast).

### Comment

Due to the predominantly black and white colour of the shells they bear a superficial resemblance to *A. fauroti*, with which they may have been confused, especially if found dead. However, they are more rounded, smaller and are closely spirally punctate on the upper whorls and between the ribs. The axial ribs are wide at the top and narrow towards the base and are smooth, not of even width and finely spirally grooved as in *A. fauroti*; the colour is between, rather than on, the main part of the ribs and the early whorls lack ribbing. The operculum is thinner and more oval. The animals live in dense colonies rather than singly.



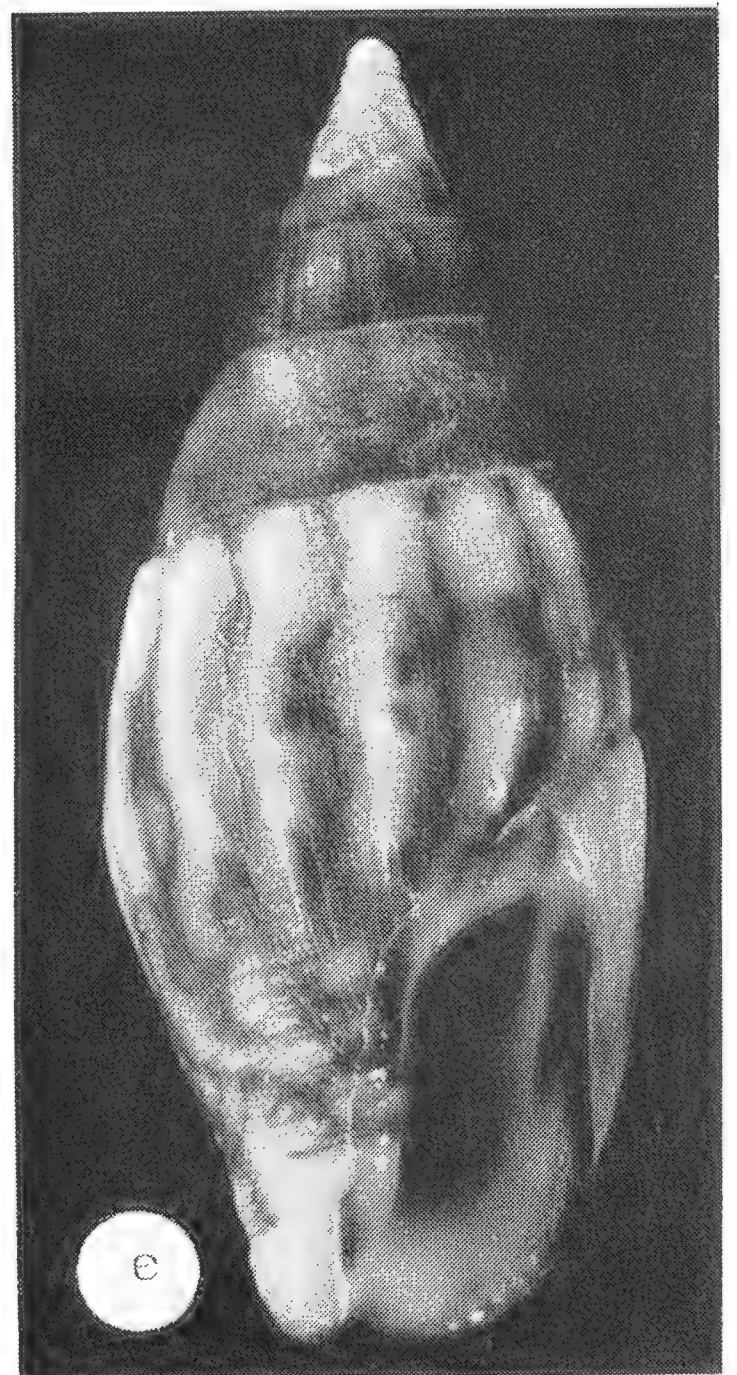
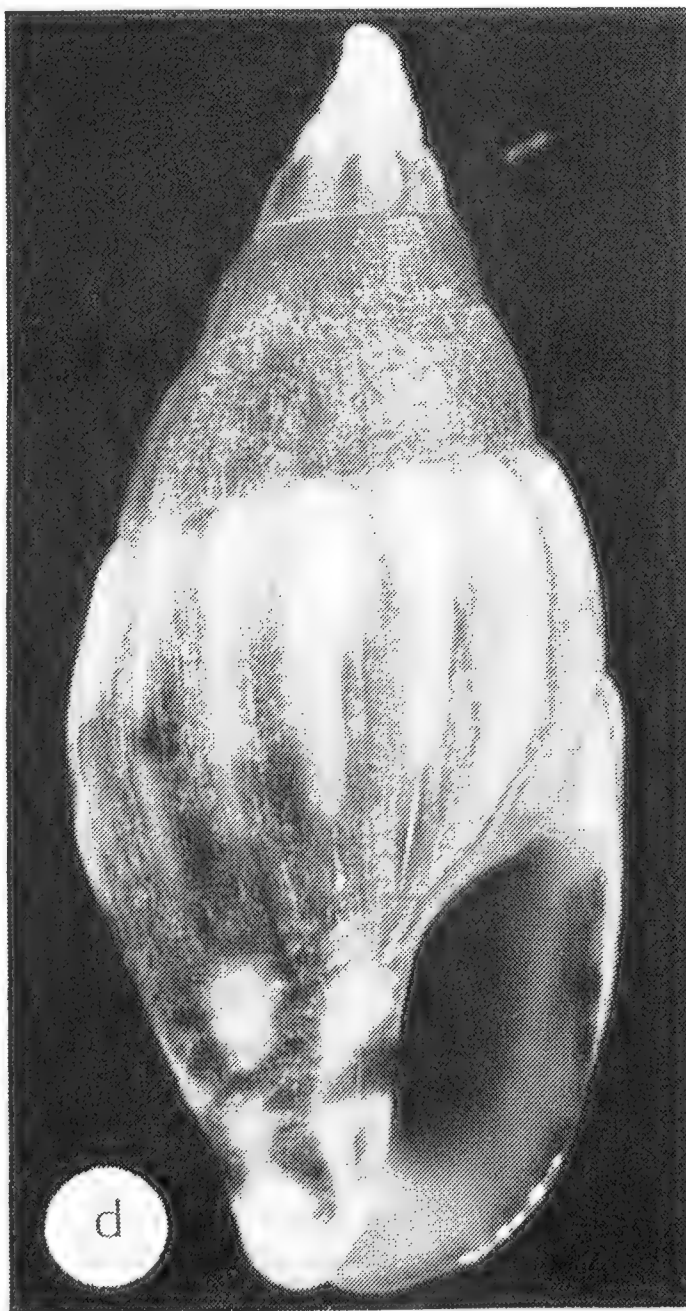
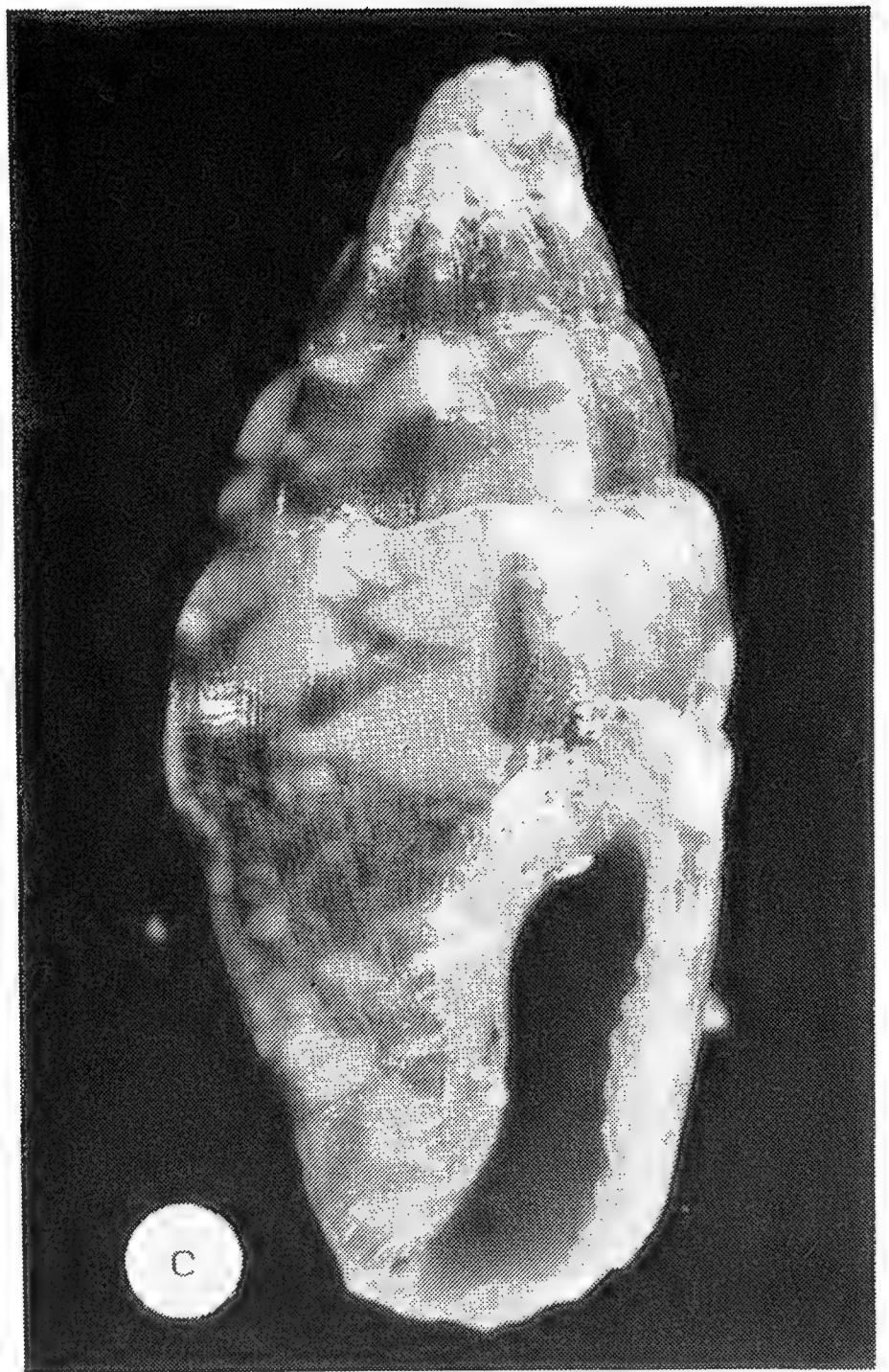
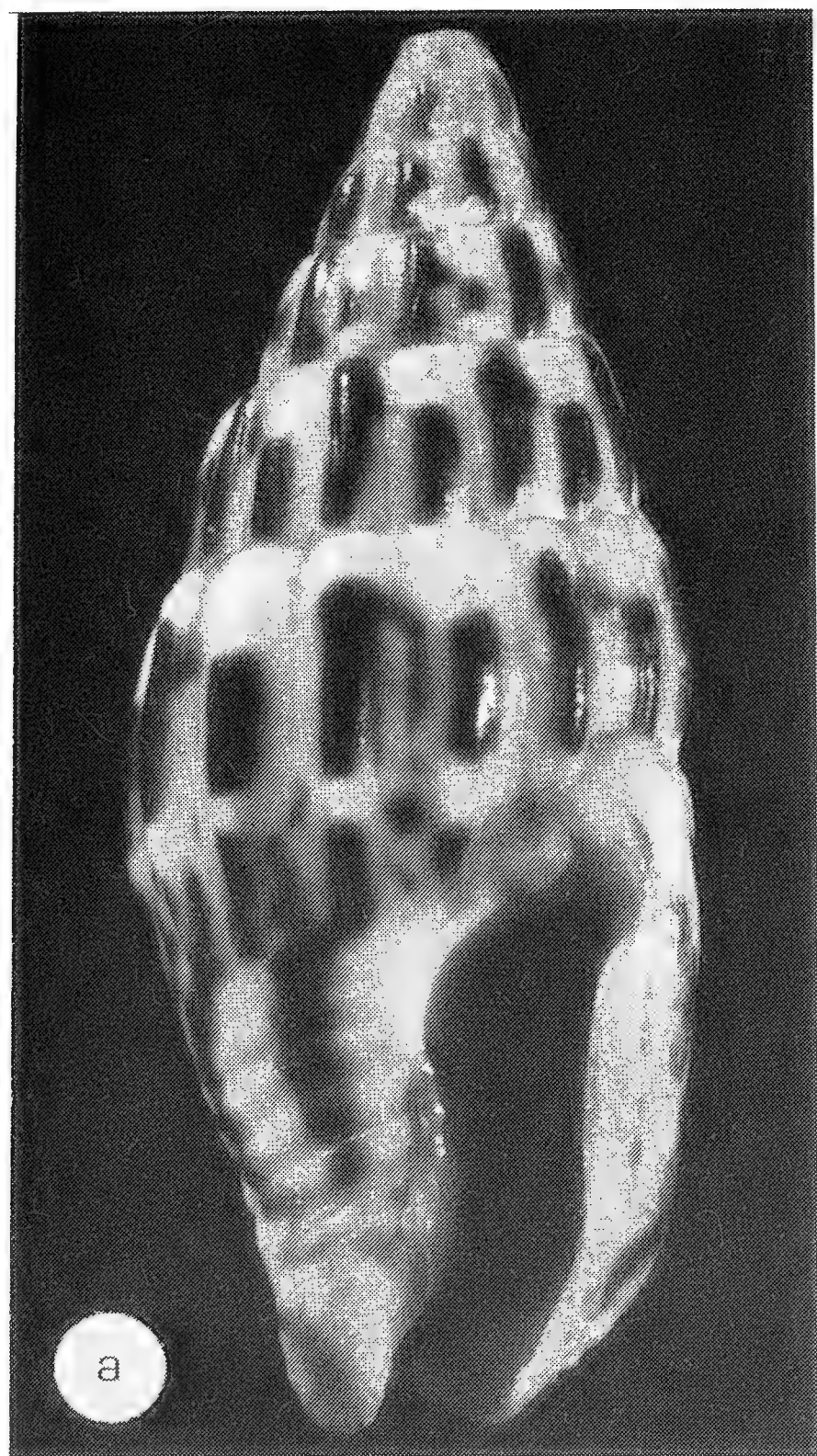


PLATE 4

a. Lectotype of *Anachis fauroti*; b. Holotype of *Anachis raysutana*; c. Paratype of *A. raysutana* (KRS collection) showing apertural denticles; d. Holotype of *Costoanachis rassierensis*; e. Paratype of *C. rassierensis* (KRS collection).



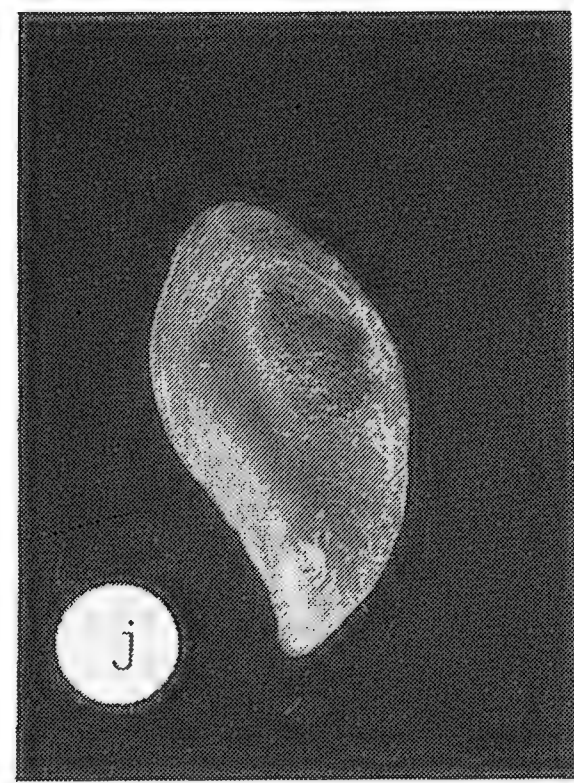
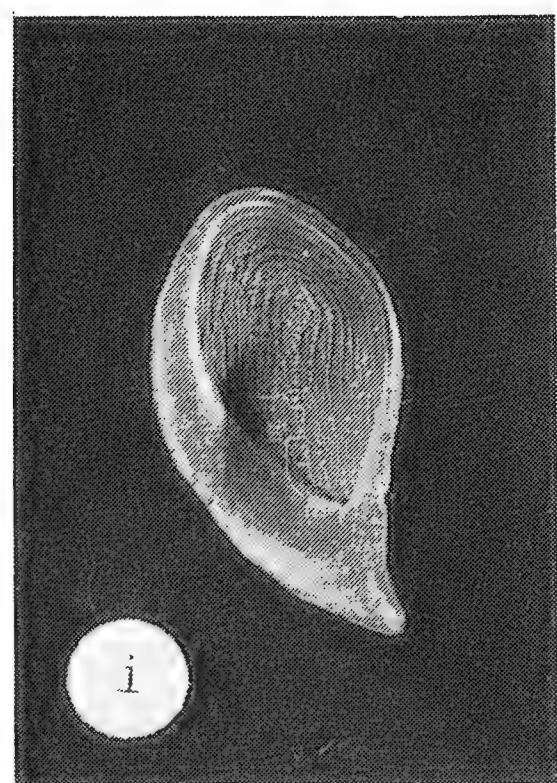
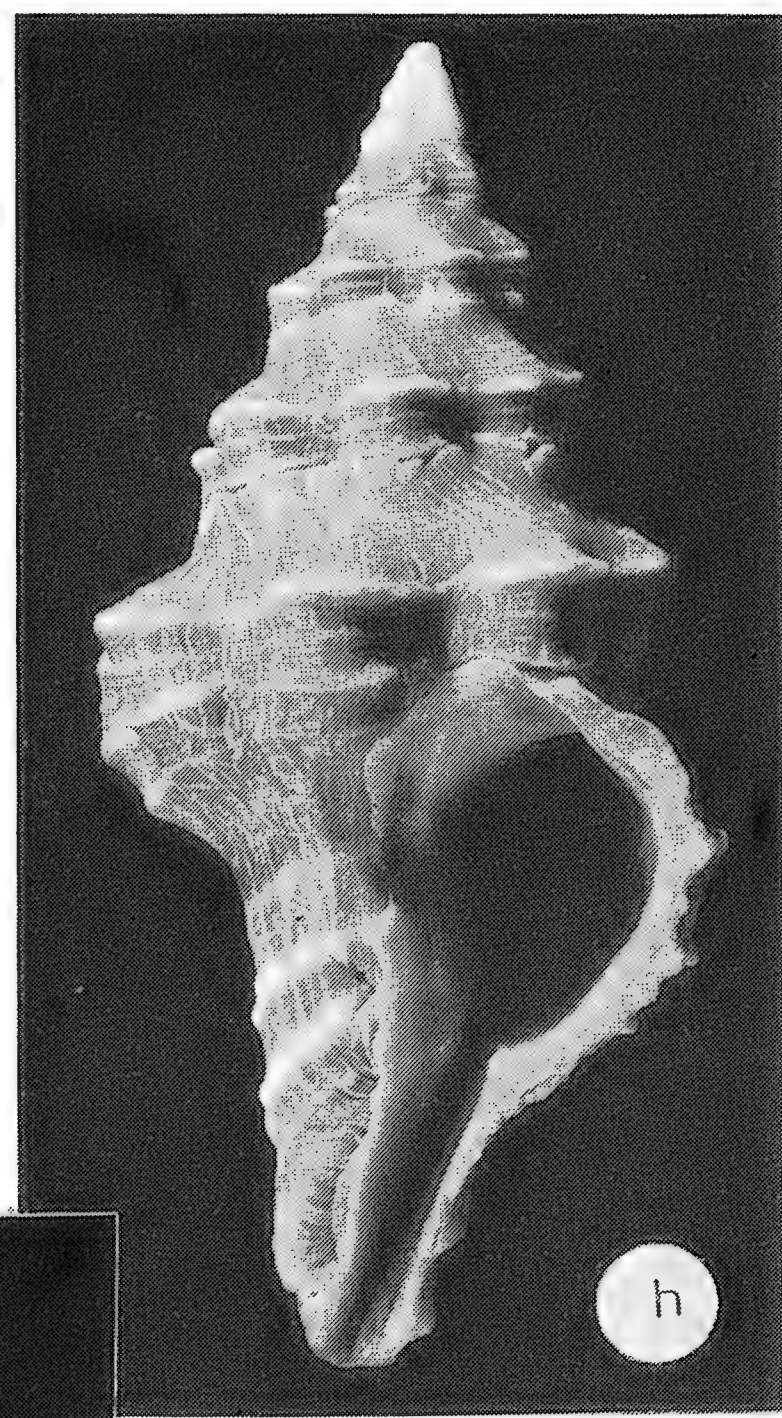
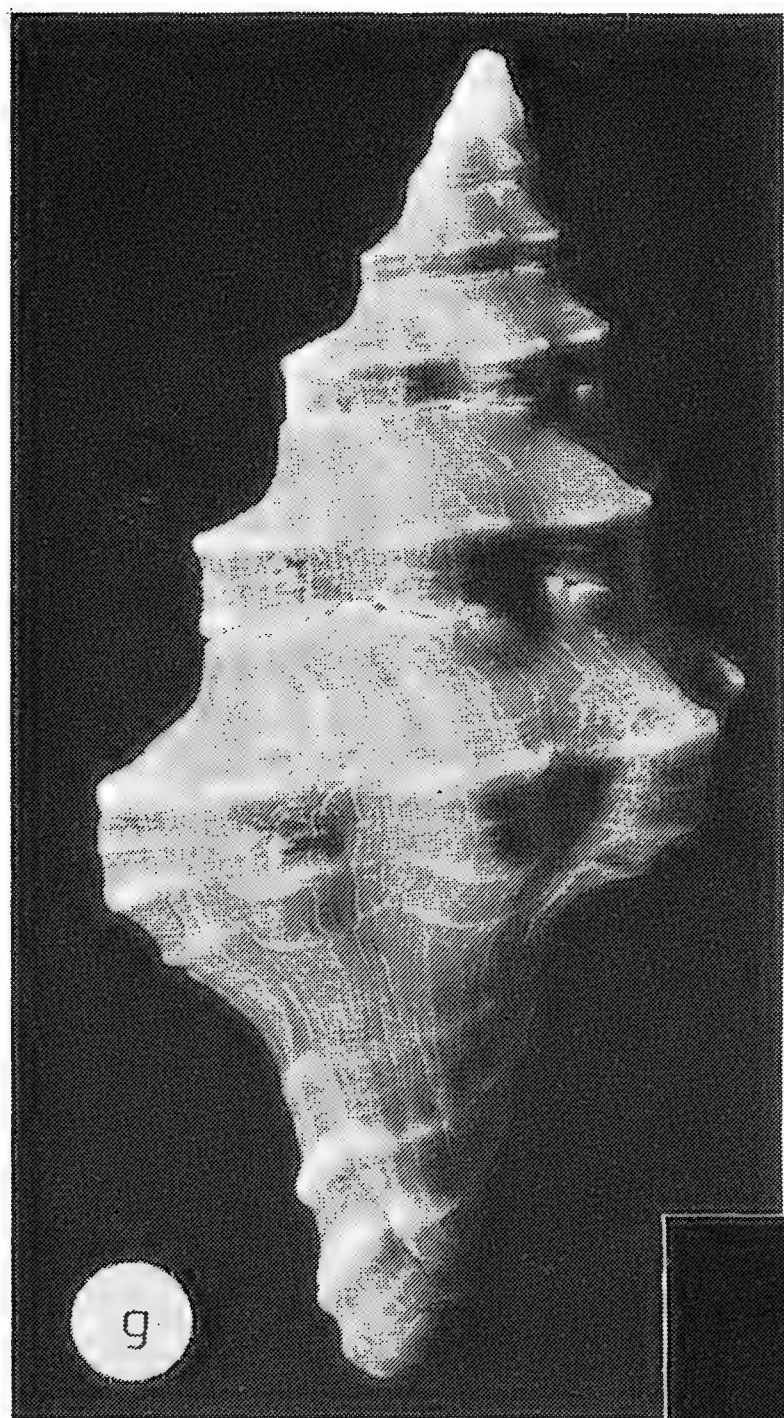


PLATE 5

f. Holotype of *Latirus bonnieae*; g, h. Paratype of *L. bonnieae* KRS collection, height 51.25 mm; i, j. Operculum of holotype.



Family Fasciolariidae

Genus *Latirus* Montfort 1810

***Latirus bonnieae*** sp nov. (Plate 5, Figs f, g & h)

*Summary of diagnostic features*

A solid, fusiform shell and a tall spire and an elongated siphonal canal. The colour is striking, the majority of the shell being a rich red-brown with a white apex and white encircling raised cords at the periphery.

*Description*

This is the *Latirus* species of Bosch & Bosch 1982.

*Shell*: fusiform, moderately solid, with an apparently sharp apex and a moderately long siphonal canal. Protoconch (Fig. 1) is in fact dome-shaped, smooth, white,  $1\frac{1}{2}$  to 2 whorls, followed by one white whorl with very fine axial ribs. In the majority of shells seen by the author the protoconch is eroded. The whorls are encircled by a strong cord at the periphery which bears 7 to 8 pointed nodules. Above this cord the shoulders are concave, below it the nodules extend into rounded ribs for a short distance and bear one fine and two coarse spiral cords. Just below these cords the body whorl narrows sharply into the neck, at the anterior of which is a strong siphonal fasciole. Above this, following the line of the fasciolar ridge are 3 to 4 coarse, gemmulated cords. In some large shells is a small pseudoumbilicus or chink. On the body whorl are many fine, close growth striae; there are a few of these striae on the other whorls. The sutures are weakly impressed.

*Aperture*: oval, extending into a long and wide anterior canal. The outer lip is thin with fine plications inside the aperture in older shells; there are two sharp plications on the columella. The columellar callus is thick, highly glazed and detached in places from the body whorl. The siphonal canal is inclined to the left.

*Colouring*: the colour is a distinctive reddish-brown (Rayner: cinnamon no. 59 to brick-red no. 62), the shell surface, columella and aperture being uniformly coloured with the exception of the conspicuous white apical whorls and the peripheral and siphonal cords which are also white.

*Periostracum*: thick, finely, longitudinally fibrous, dark brick (Rayner: no. 60).

*Operculum* (Plate 5, Figs. i, j): thick and horny, lanceolate with the nucleus at the pointed end which is sharp, very fine, numerous growth striae externally. It is convex on the exterior and incurved considerably at the apex and upper edge. Colour sepia. Internally the muscle scar is deeply incised round the edge, heavily grooved and dull; otherwise the varnish layer is glazed. The edges are thickened.

*Animal and Habitat*: unknown.

*Etymology*: named for Bonnie, daughter of Dr. and Mrs. Donald T. Bosch, who helped her parents on many shell collecting expeditions before her marriage.

*Size*: of eight shells measured the average height was 52 mm, diameter 26 mm, body whorl height 35.6 mm and aperture height 28.5 mm. The largest shell was 60 mm, the narrowest 49.5×23.25 and the broadest 47.5×25.5. The body whorl is approximately 66% the height of the shell and the aperture approximately 57% the height.

*Holotype*: BMNH registered number 1984078., leg. D. T. Bosch, east coast of Masirah Island. Height 54 mm, diameter 26 mm, aperture length 28 mm. Operculum 12×6.75 mm.

*Paratypes*: ONHM Accession number 1984/68/A; NMW Accession number 1984.046.



Other paratypes are in the collection of the Zoölogisch Museum, Amsterdam, and with Dr. and Mrs. Bosch and the author.

*Known Distribution:* Masirah Island, Oman.

### *Comment*

All the specimens seen by the author came from the collection of Dr. and Mrs. Bosch who said that they had had a total of about sixty specimens altogether, many very worn, all cast up, probably along the east coast of Masirah south of Ras al Ya (Rassier). Over a period of some twenty eight years of collecting on Masirah they have found a few shells nearly every year. The operculum of the holotype came from a heavily encrusted shell given to the author in 1982. After some months it was found to be smelling strongly with much decomposing matter oozing from it. The operculum, attached to part of the foot, was washed out from it, but, despite careful sieving and searching through the rest of the decomposing matter the radula was not found. The animal was probably cast up alive as the operculum was withdrawn so deeply as to be invisible, and almost certainly in December/January 1982 otherwise it would have decomposed earlier. Despite searches by the Bosch family, helpers and friends and myself live animals have not been found. Possibly it is a deep water species.

This new species resembles *L. polygonus* (Gmelin) in shape but it differs in colour, in the character and lesser number of the spiral cords, in the aperture and canal being shorter and in the operculum being paler in colour and comparatively broader (this comparison made with a shell in the author's collection). *L. cingulifera* (Lamarck) and *L. recurvirostris* (Schubert & Wagner) have much stronger and more numerous spiral cords and the shape of the whorls is different.

### DISCUSSION

Of the four species in this paper, *A. fauroti* is the only one to have been recorded from outside Oman: the remainder have not been recorded from outside the areas of Masirah and Dhofar. *A. fauroti* was described from Obock, Djibouti (then French Somalia) and its range extends certainly as far East as the Mekran coast and into the Arabian Gulf; on the Arabian side from the Mussandam to Abu Dhabi and on the Iranian side from Hormuz to Tahiri. It lives on rocks or stones or in rocky areas with patches of silt or sand; these areas are either exposed or sheltered. If I am correct in assuming that the shell referred to by Sturany (1903) as *C. (A.) terpsichore* Sowerby is in fact *A. fauroti*, it extends into the Red Sea as far as Ras Ruwai north of Port Sudan (22°21'N, 36°30'E).

To date the three new species of Buccinacea described here have been found only in the areas of Masirah and Dhofar, south-west of Ras al Hadd. Many other molluscs appear to be restricted to this area including *Fusinus (Sinistralia) gallagheri* Smythe & Chatfield 1981. These areas are affected by the south-west monsoon as far north as Ras al Hadd and are also affected by the upwellings of cold water from the depths (this is discussed in Taylor and Smythe 1985). The granite outcrops of Dhofar from Mirbat to Hasik and the Kuria Muriya Islands are close to areas of upwelling; the rest of Dhofar and Masirah are possibly not so greatly affected by them as they occur further off shore.

The range and habitat of *Latirus bonnieae* is so far unknown but it seems likely that it will be found to the south-west of Masirah; *A. raysutana* occurs on the softer rocks of Dhofar and

## SMYTHE: OMAN BUCCINIDS

Masirah, *C. rassierensis* occurs on the harder rocks. In Dhofar this last species is found in the regions inhabited by *Haliotis mariae* (Gray), *Trochita dhofarensis* Taylor & Smythe several unidentified species of Chiton and other unidentified molluscs.

## ACKNOWLEDGEMENTS

The author would like to thank H.R.H. Sayyid Faisal bin Ali Al-Said, Minister of National Heritage and Culture, H. E. Malallah bin Ali Habib, Under-Secretary of the Ministry, Sheikh Said al Fatimy, Director of the Oman Natural History Museum and Mr. Michael D. Gallagher for arranging visits to Oman in general and Dhofar in particular and for much help and advice. Thanks are also due to Dr. and Mrs. D. T. Bosch for hospitality and help, to Dr. Saini of the Health Centre for hospitality and help on Masirah, to SOAF for flights to and from the island and to Mr. R. H. Daly, Government Adviser for the Conservation of the Environment. The author is grateful to the staff of the British Museum (Natural History), especially to Ms. K. M. Way and Dr. J. D. Taylor, to the staff of the Muséum National d'Histoire Naturelle, Paris for the loan of type material, to Dr. P. G. Oliver and Miss Alison Trew of the National Museum of Wales for facilities and help, to Mr. Kevin Boot of the Royal Albert Memorial Museum, Exeter for making the Shopland collection available for study and to Dr. H. K. Mienis, Dr. H. Coomans and Dr. R. Moolenbeek for advice.

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# A NEW SUBSPECIES OF *CONULINUS UGANDAE* (VON MARTENS) FROM KENYA (PULMONATA: ENIDAE)

BERNARD VERDCOURT<sup>1</sup>

(Accepted for publication, 20 October 1984)

*Abstract:* *Conulinus ugandae costatus* ssp. nov. is described from N. Kenya.

When I gave a synopsis of the genus *Conulinus* Von Martens (Verdcourt 1966) I left undescribed what I then considered to be several taxa known only from poor specimens. Further material has now been examined enabling a decision to be made and a new subspecies to be described.

## ***Conulinus ugandae costatus* n. subsp.**

1923 *Conulinus percivali* Germain, p. 65, pl 2, fig. 56 (in synonymy)

1966 *Conulinus ugandae* n. subsp. Verdcourt, p. 285

1966 *Conulinus ugandae* forma? Verdcourt, p. 285, fig. 6

1966 *Conulinus* sp. Verdcourt, p. 286, fig. 5

Differing from subsp. *ugandae* in the much more evident sculpture on the body whorl and spire. Apical whorl with very fine spiral striae and next  $1\frac{1}{2}$  whorls with excessively fine transverse striae, about 300 per mm; rest of whorls with coarse curved ribs, about 3–5 per mm.

I have come to the conclusion that the differences in shape which cautioned me to suggest three taxa were involved are of no real significance. Unfortunately no material of the animal is yet available despite the recent greatly increased accessibility of Marsabit.

KENYA. Uaraguess (Urguess, Uraguess, Warguez etc.), no collector but probably Percival (BM 1912.8.18. 58–60 and 1937.12.30. 2145–2147 including proposed types of an undescribed Preston species one named after the locality and another Latin for ‘brother’); same locality, Percival (BM 1912.8.18. 61–62 and 1937.12.30. 2148 including proposed type of an undescribed Preston species named after the collector (two of the above lots had been identified as *C. daubenbergeri* by Connolly and another as *C. ugandae*). Mt. Marsabit, collector unknown, probably Percival (Liverpool Museum 1965.141. holotype and 3 paratypes); same locality, Gof Bongole, 16 Jan. 1975, Å. Anderson (Natural History Museum, Stockholm); same locality, collector not known (Zoological Museum, Amsterdam, ex. coll. J. R. Le B. Tomlin); same locality, Aug. 1957, B. Verdcourt (National Museum, Nairobi).

<sup>1</sup> Spring Cottage, Kimbers Lane, Maidenhead, Berks.

Germain (loc. cit.) mentions a *Conulinus percivali* and gives a good figure but definitely says 'qui est synonyme du *Mabiliella daubenbergeri* Dautzenberg'. The specimen is preserved in the Museum National d'Histoire Naturelle, Paris.

A specimen (BM 1937.12.30. 2150) collected by R. Kemp in Kampala, Uganda was the proposed type of an undescribed Preston species to be named after the city. This shows distinct signs of costae and is the only southern specimen I have seen to do so. There is no reason to doubt the locality and it has influenced me in deciding the status of the taxon treated in this note. The tendency to ribbing is present in all *Conulinus* but not visible in most species until the shell is very worn; in the forested mountain tops of Marsabit and the Mathews Range, populations have arisen where it is much accentuated and until adequate material is available for dissection I have preferred to refer them to a subspecies.

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# A NEW SPECIES OF *TROCHITA* (GASTROPODA: CALYPTRAEIDAE) FROM OMAN: A RELICT DISTRIBUTION AND ASSOCIATION WITH UPWELLING AREAS

JOHN D. TAYLOR<sup>1</sup> AND KATHLEEN R. SMYTHE<sup>2</sup>

(Accepted for publication, 20 October 1984)

**Abstract:** A new species of the calyptraeid gastropod *Trochita* is described from southern Oman. The species lives limpet-like, upon exposed rocky headlands, in an area strongly influenced by cold upwelling waters. *Trochita dhofarensis* is most similar to the mainly West American *T. trochiformis* and *T. spirata*. A Miocene distribution pattern disrupted by the closure of the Mediterranean/Indian Ocean seaway is the most parsimonious explanation of the disjunct distribution pattern. *Trochita* species appear to be associated with cold upwelling current systems in the Atlantic, Pacific, Indian and Southern Oceans.

## INTRODUCTION

The marine organisms of the southern shores of the Arabian Peninsula are amongst the least known in the world. Nevertheless, a few recent publications (Bosch & Bosch 1982, Mienis 1978, Smythe 1980, Smythe & Chatfield 1981) suggest a considerable endemism in the molluscan fauna of the area.

A feature of particular interest along this coast is the seasonal cold upwelling system associated with the S.W. Monsoon which blows from May to October. This results in cold, nutrient-rich waters being brought to the surface close to the shore, effecting a depression of the surface water temperature by about 6° C. Although some of the oceanographic features of this upwelling system have been investigated (Currie, Fisher & Hargreaves 1973), there have been no studies of the littoral and shallow sublittoral organisms within the area of the upwelling system. However, in 1983 a survey of shores in the Salalah area was made by the Tropical Marine Research Group of York University and the preliminary results reported in Barratt, (1984).

Along some parts of the southern Oman coastline the edge of the continental shelf lies within 10 km of the shore and here the effects of the upwelling on the coastal organisms are most noticeable. One such area includes the metamorphic rock promontory between Mirbat and Hasik about 60–120 km east of Salalah (Fig. 1). This area differs from other shores in the area because the shallow sublittoral zone is dominated by seasonal growths of brown algae, including the southern kelp *Ecklonia*, with a coralline algal understory. *Ecklonia* is normally found in temperate areas of Australia, New Zealand and South Africa. A number of unusual molluscs have been found associated with this anomalous flora, the most conspicuous being the large abalone *Haliotis mariae* Gray. Large haliotids are also normally associated with temperate waters such as around Australia, Japan, South Africa, California, and the N.E. Atlantic. The biota of this area is in fact more similar to that of the warm temperate zones (e.g. Brown & Jarman 1978) than to adjacent tropical shores.

<sup>1</sup> Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

<sup>2</sup> 6, Blondell Drive, Bognor Regis, West Sussex, PO21 4BQ

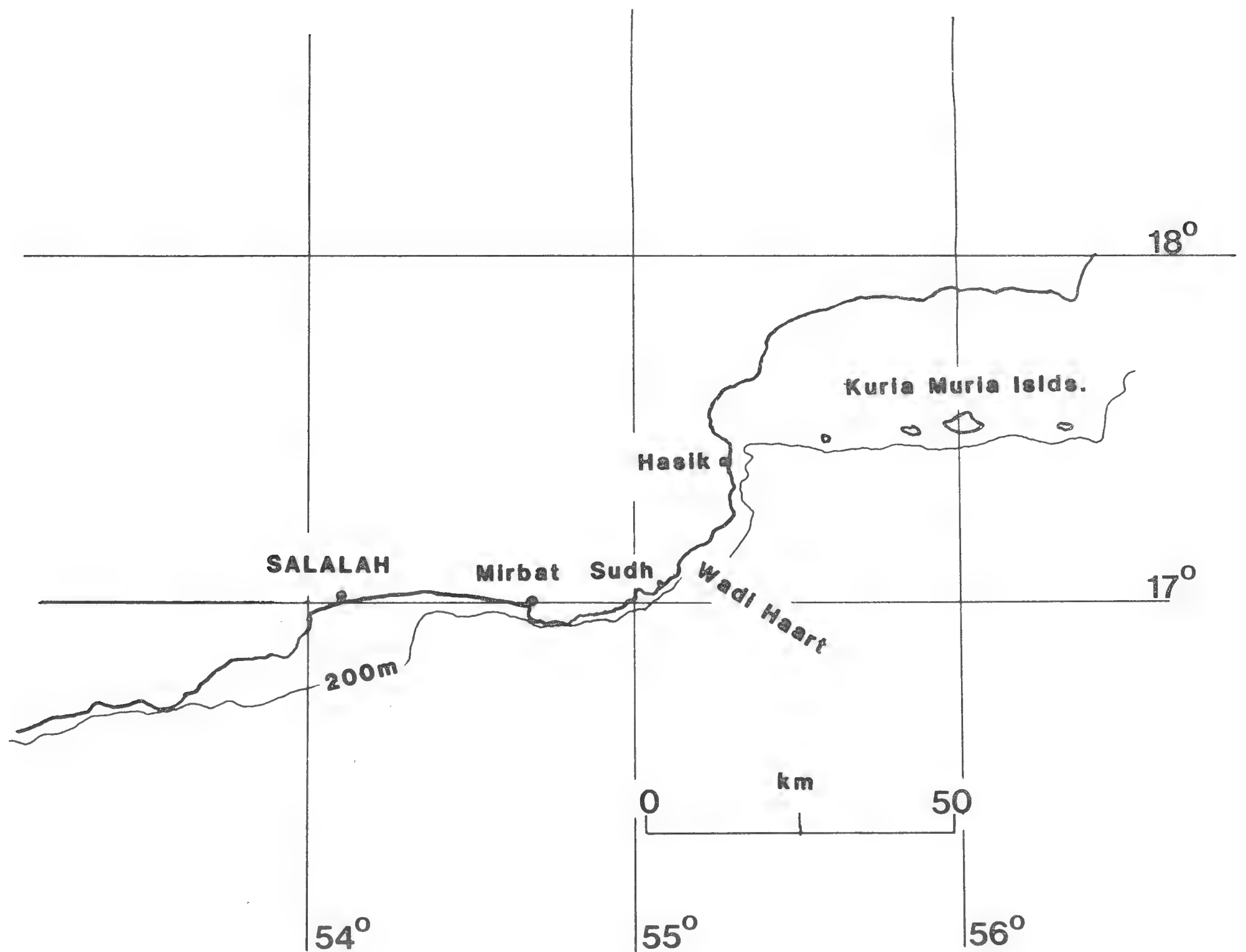


Fig. 1. Sketch map of the southern Oman coast near Salalah showing the main localities mentioned in the text.

One of the most notable molluscs inhabiting the low intertidal and shallow sublittoral zones of the area is an undescribed species of the calyptraeid gastropod *Trochita*. Species of this genus are normally associated with the West American area and the occurrence in Oman is thus of some zoogeographical interest. This species was found independently by the two authors and is described below.

#### SYSTEMATIC DESCRIPTION

Family Calyptraeidae

Genus *Trochita* Schumacher 1817 (type species: *Trochita spiralis* Schumacher, 1817 (= *T. trochiformis* Born 1778); S. D. Rehder, 1943)

***Trochita dhofarensis*** Taylor & Smythe (Plates 6 & 7; text Figs. 2–4)

#### *Diagnosis*

Shell trochiform, squat, four whorls, with aperture forming the entire base of shell; coarse axial, rounded ribbing. Shell colour buff, with chocolate brown aperture.

*Description*

Shell squat ( $H/W=0.41\pm0.06$ ,  $n=27$ ), four whorls, apical angle  $100^\circ$ , mean shell width  $30.8\pm8.9$  mm, ( $n=40$ ), largest shell 52.1 mm. Some specimens with an angular shoulder towards the adapical edge of each whorl. Aperture large and circular, forming entire abapical portion of the shell. Edge of aperture highly tangential and slopes at an angle of  $97^\circ$  to the axis of coiling so that shell sits flush, limpet-like, against the substrate. Coarse axial ribbing prominent, with the ribs rounded and rather rugose; interspaces between the ribs are also rounded. In juveniles the interspaces are wider than the ribs but in most adult shells the ribs are generally broader than the interspaces. Most ribs extend across each whorl but a few originate in the interspaces about midway across each whorl. The number of ribs increases with shell size (Fig. 2) and number around 32–34 in average sized shells (30.0 mm shell width). In most shells the ribbing of the first two whorls is inclined obliquely at an angle of  $120$ – $130^\circ$  to the coiling axis, whilst on later whorls the ribs lie on a plane through the axis. Apertural area or base of shell concave, columellar thin, plate-like and glossy.

*Colour*: Exterior of the shell buff, juveniles have brown interspaces between the ribs and sometimes brown mottling. Apertural area and base of shell chocolate brown.

*Animal*: Foot creamy yellow, large, flat and limpet-like. Snout short and wide (Fig. 3); when closed the mouth is a vertical slit; tentacles with eyes on basal bulge. On either side and ventral to the head are large semicircular flaps, the propodial folds. The edge of the mantle skirt is thickened and lobed. The left hand side of the opening to the mantle cavity with a row of short pallial tentacles. Dorsal surface of head and tentacles dark grey, underside light grey. Mantle cream with grey fringe to mantle skirt. The mantle cavity is long and coiled with the ctenidium extending almost the whole length (Fig. 4). The animal is very similar to *Trochita trochiformis* described (as *T. radians*) by Kleinstüber (1913) and to *Crepidula* (Fretter & Graham 1962).

*Radula*: taenioglossan, 2–1–1–1–2. (Pl. 2)

Cusp formulae (see Hoagland 1977): central  $3-1-3/0-0$  to  $3-1-2/0-0$ ; lateral  $1-1-8/0-0$  to  $3-1-6/0-0$ ; inner marginal  $6/5$  or  $6/6$ ; outer marginal  $6/0$ .

*Types*

*Type locality*: Ras Mirbat, Dhofar Province, Oman ( $16^\circ58'N$ ,  $54^\circ52'E$ ).

*Holotype*: British Museum (Natural History) Reg. No. 1984067 Height 19.0 mm, width 40.1 mm.

*Paratypes*:

B.M.N.H.:

19 preserved animals and 31 dead shells from Wadi Haart:  $17^\circ04'N$ ,  $55^\circ06'E$ .

Oman Natural History Museum:

60 dead shells, Accession No. 1984/69, from headlands south of Mirbat:  $16^\circ58'N$ ,  $54^\circ42'E$  &  $16^\circ57'N$ ,  $54^\circ43'E$ . Khawr Maratma:  $17^\circ03'N$ ,  $55^\circ05'E$ . Wadi Sath:  $17^\circ03'N$ ,  $55^\circ00'E$ .

*Other material*

B.M.N.H.:

1 preserved animal from Hasik:  $17^\circ04'N$ ,  $55^\circ15'E$ .

1 preserved animal from Ras Mirbat:  $16^\circ58'N$ ,  $54^\circ52'E$ .



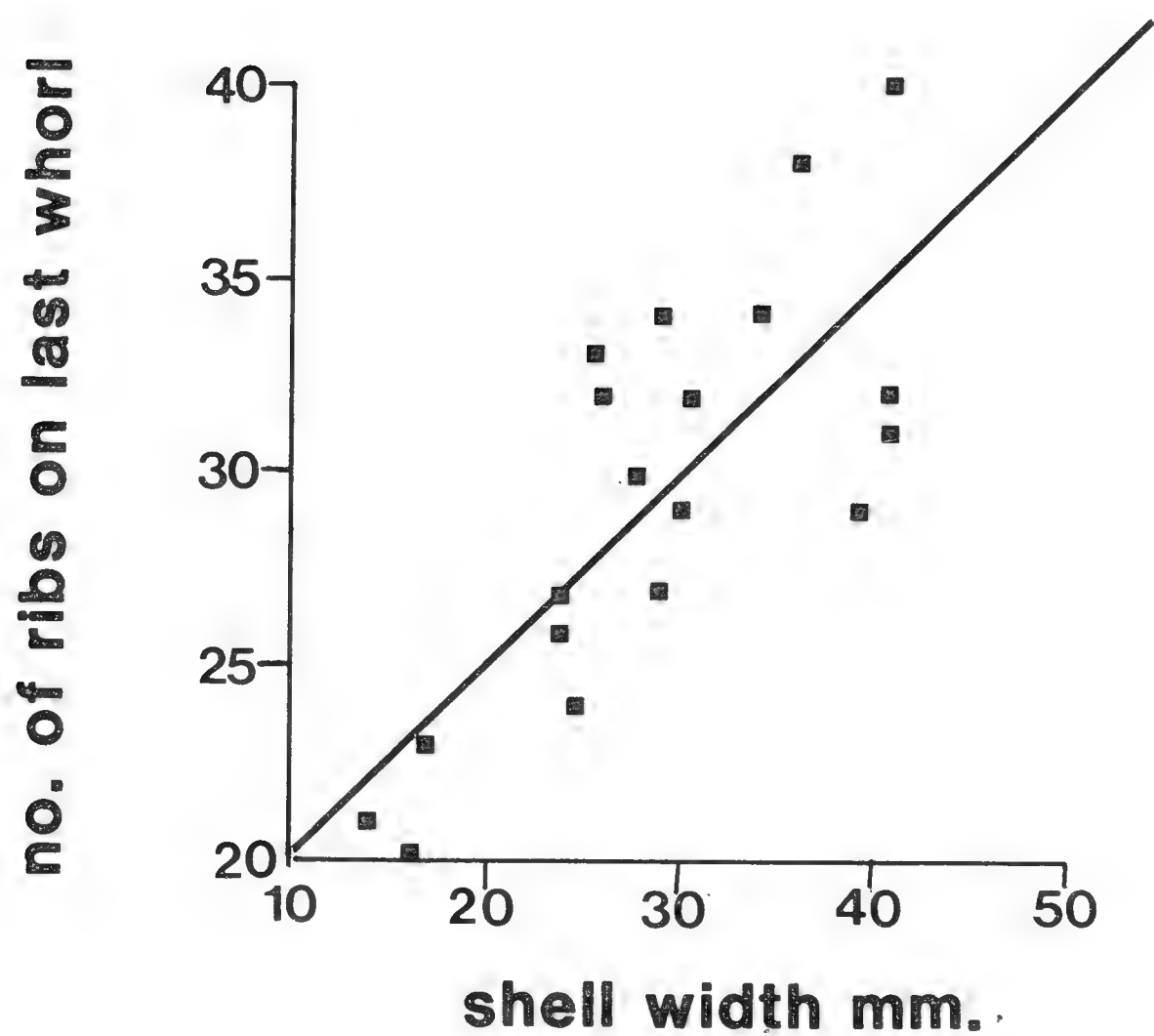


Fig. 2. Relation between number of ribs and shell size in *Trochita dhofarensis*. Regression:  $y = 0.48x + 15.5$ .

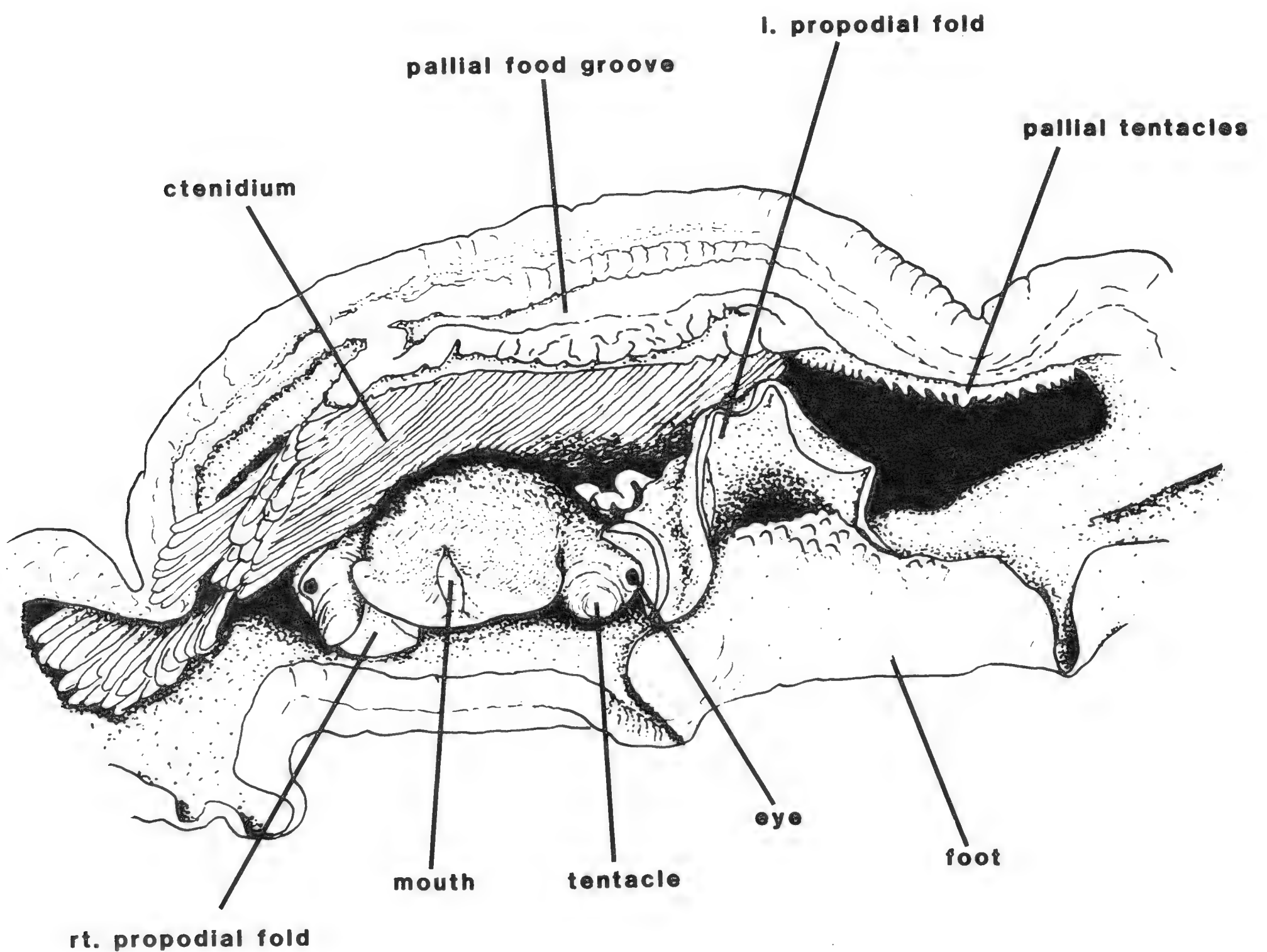


Fig. 3. *Trochita dhofarensis*: animal from the front. Mantle has been slightly pulled back to expose head.

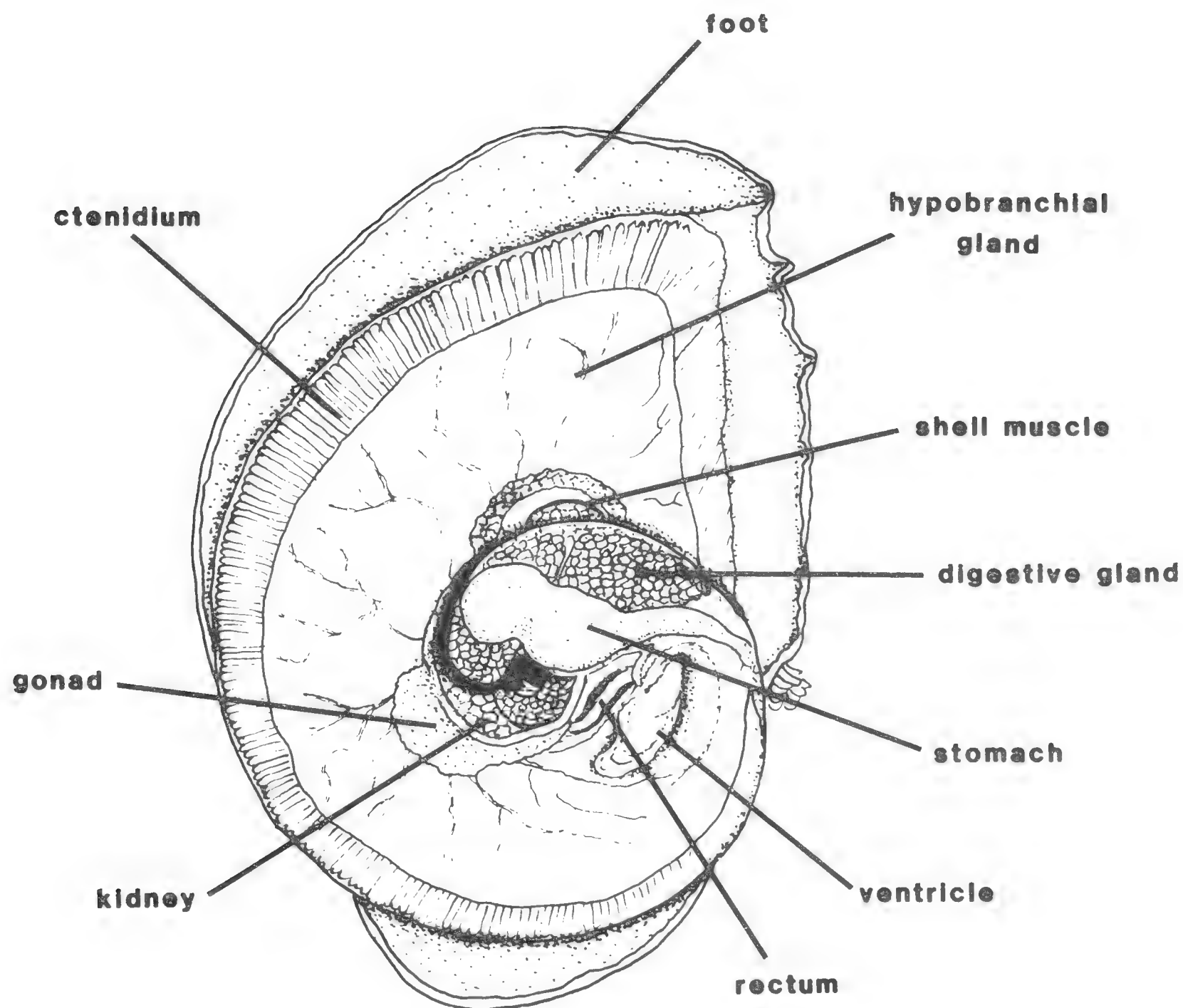


Fig. 4. Dorsal view of *Trochita dhofarensis* with the shell removed.

1 dead shell from Al Halaniya, Kuria Muria Islands, collected by M. D. Gallagher 1978: 17°30'N, 56°00'E.

K. R. Smythe Collection:

9 live collected shells from type locality.

#### *Comparison with other species*

Some of the major morphological features of the living *Trochita* species are given in Table 1. *Trochita dhofarensis* is most closely similar to *T. trochiformis* (Born 1778) but differs in having rounded ribs, a brown aperture, no visible periostracum and the possession of cusps on the inner margins of the lateral teeth of the radula. *T. trochiformis* also grows much larger (85–100 mm) than *T. dhofarensis*. The other somewhat similar species is *T. spirata* (Forbes 1852) which has a higher translation rate of coiling, reflected in the higher H/W ratio and three rounded whorls. Keen (1971) lists a third species *T. ventricosa* Carpenter 1857, which she distinguishes on the basis of the white aperture and angular whorls. However, the holotype illustrated by Keen (1972, Fig. 55) has angular whorls and coarse ribs and although the columella is white the rest of the aperture is brown. The specimen is a juvenile and in our opinion shows great resemblance to the early whorls of some *T. spirata* and we regard it as an ecophenotype of that species.

TABLE 1

Comparison of the major morphological characters of *Trochita* species

	<i>dhofarensis</i>	<i>trochiformis</i>	<i>spirata</i>	<i>pileus</i>	<i>helicoidea</i>
Number of whorls	4	4	3	3	3
Umbilicus	absent	absent	absent	present	present
Periostracum	transparent	brown	?	brown	?
Ribbing strength	coarse	coarse	coarse	fine	medium
Ribbing angle	radial	radial	radial	oblique	oblique
Ribbing shape	rounded	angular	angular	angular	scabrous
Shape H/W	0.41±0.06	0.41±0.05	0.6±0.07	0.51±0.08	0.51±0.03
	n=27	n=12	n=4	n=10	n=8
Colour of aperture	brown	white	brown	white	white
Cusps on inner margin of radular teeth	present	absent	?	absent	?

*Habitat*

*Trochita dhofarensis* has been found live only at localities between Ras Mirbat and Hasik to the east of Salalah, and dead shells all along this part of the coast as well as on the Kuria Muria Islands. All of these sites are associated with areas of cold upwelling and on present evidence it seems that *Trochita* is restricted to upwelling sites.

The gastropod is found in aggregations in crevices in the low intertidal and shallow sublittoral zones of exposed rocky headlands. In the shallow sublittoral, down to a depth of at least 4 m the gastropods live upon open rock surfaces. The animals cling limpet-like, leaving a scar with a thin calcareous secretion. The shells of intertidal specimens are heavily encrusted with coralline algae and vermetid gastropods and considerably eroded by the boring sponge *Cliona*.

## DISCUSSION

Two other species of *Trochita*, *T. trochiformis* and *T. spirata*, are found on the west coast of south and central America (Fig. 5); *T. trochiformis* ranges from Manta, Ecuador to Valparaiso, Chile and *T. spirata* from Mazatlan to the Gulf of Tehuantepec, Mexico (Keen 1971). *Trochita pileus* (Lamarck 1822) is found from the Straits of Magellan to northern Argentina (Rehder 1943) and *Trochita helicoidea* (Sowerby 1883) lives on the southern tip of South Africa between Jeffreys Bay and East London (Kilburn 1982). Specimens very similar to and probably conspecific with *Trochita trochiformis* have been found at the Cape Verde Islands and Benguela, Angola (Rehder 1943, Nicklès 1950, von Cosel 1982, B.M.N.H. collections).

Fossil *Trochita* have been found in Miocene and Pliocene deposits of the Santa Barbara area of California (Grant & Gale 1931); in the Lower Miocene Gatun Formation of the east side of the Panama Isthmus (Woodring 1957); in the Miocene of Venezuela (Jung 1965); the Pliocene of Trinidad (Jung 1969); and from the Plio-Pleistocene of Morocco and the Cape Verde Islands (Lecointre 1952, Nicklès 1950). An extensive search of the literature and collections failed to reveal any occurrence of *Trochita* in the Neogene deposits of the Mediterranean area. This would have provided a link between the Oman area and the





Fig. 5. Map showing the distribution of *Trochita* species. Sites where fossil *Trochita* have been found outside of the present-day range are marked by a triangle. See text for details.

Atlantic. However if the association of *Trochita* species with upwelling areas, discussed below, is correct, then the absence of such areas in the Mediterranean would account for this.

The Oman species *Trochita dhofarensis* is morphologically closely similar to, and thus considered related to the west American *T. trochiformis* and *T. spirata* and to the Cape Verde specimens. It is less similar to the Magellanic *T. pileus* and the South Africa *T. helicoidea*.

There are two interesting features of the biogeography of *Trochita* species; firstly there is the disjunct distribution pattern with representatives in the East Pacific, Atlantic and N.W. Indian Oceans and secondly there is the association of *Trochita* species with cold, upwelling current systems.

The present day distribution of *Trochita* species presents a problem. An explanation based upon either present-day or past dispersion processes would be complex, particularly as the Magellanic and South African species are not very similar to *T. dhofarensis*. A more probable explanation is that *Trochita* once had a much broader geographical range in the ancient Tethyan Ocean and the two vicariant events of the formation of the central American isthmus and the closing of the connection between the Mediterranean Sea and Indian Ocean geographically isolated the species. The central American isthmus was formed in the Pliocene (Marshall 1983) and the closing of the Mediterranean/Indian Ocean connection occurred either in the Lower Miocene (Adams *et al.* 1983), or less likely, in the upper part of the Middle Miocene (Rogl & Steininger 1983). The Upper Miocene salinity crisis in the Mediterranean (Raffi & Marasti, 1982) eliminated all benthic molluscs, the Sea being recolonised from the Atlantic. The present-day

distribution of *Trochita* is thus, apparently, a relict of at least a Lower Miocene distributional pattern.

The southern species *T. pileus* and *T. helicoidea* are more similar to species of the southern Australian and New Zealand genus *Sigapatella*. The early whorls of *T. pileus* resemble the adult shells of *Sigapatella* and a derivation by neotony of the genus from a *T. pileus* type ancestor is possible. The S. American, S. African and S. Australian forms are united by the eastward flowing Southern Ocean current system.

The second notable feature of the distribution of the *Trochita* species is the association with cold upwelling current systems. In addition to the occurrence of *Trochita dhofarensis* in the Arabian Sea upwelling system, *T. trochiformis* is associated in the Pacific with the Peru Current, and in the Atlantic, at the Cape Verde Islands and Angola with upwellings produced by the Canary and Benguela currents respectively. *Trochita spirata* occurs in West Mexico which is influenced by the southern end of the California upwelling system and a smaller, seasonal upwelling in the Gulf of Tehuantepec (Smith 1968). The distribution of the South African species *T. helicoidea*, coincides with an inshore, small-scale, seasonal upwelling near Port Elizabeth caused by the deflection offshore of the Agulhas Current and south easterly summer winds (Bang 1970). The Magellanic species *Trochita pileus* is not associated with an upwelling system but occurs in an area influenced by the cold Falklands Current which flows northwards along the coast of Argentina.

It could be argued that the *Trochita* once had a much broader habitat distribution and has become restricted to upwelling areas as refuges. However, the fossil evidence suggests that during and since the Miocene, *Trochita* has been associated with upwelling sites. That is, the Californian fossils may have been associated with the Californian upwelling system; the Venezuela records with upwellings on the north Venezuelan coast and the Moroccan fossils with the Canary Current upwelling.

The sublittoral flora and fauna of the Mirbat-Hasik area of southern Oman is anomalous; an enclave of temperate water organisms including kelp and large abalones surrounded by tropical biota. The *Trochita* evidence suggests that the upwelling system of this coast has been present at least since the Lower Miocene.

The relict fauna described from northern Venezuela by Petuch (1981) is perhaps analogous; here Meso- and Neogastropod species considered extinct since the Miocene are surviving today in an upwelling area. The cold water masses are thought to offer a physiological barrier to the colonisation of warm water species, and the surrounding warm waters form a barrier to the dispersal of the cold-water adapted forms. Similarly, Houvenaghel (1978) also suggests that a crown of upwelling water around the Galapagos Islands presents a water barrier to immigration from outside of the Archipelago.

There have been few studies of the benthos associated with upwelling areas (see Thiel 1978), but the relict fauna described by Petuch (1981) and the initial results of the Oman study suggest that the biota of these oceanographic 'islands' is of considerable biogeographical and evolutionary interest.

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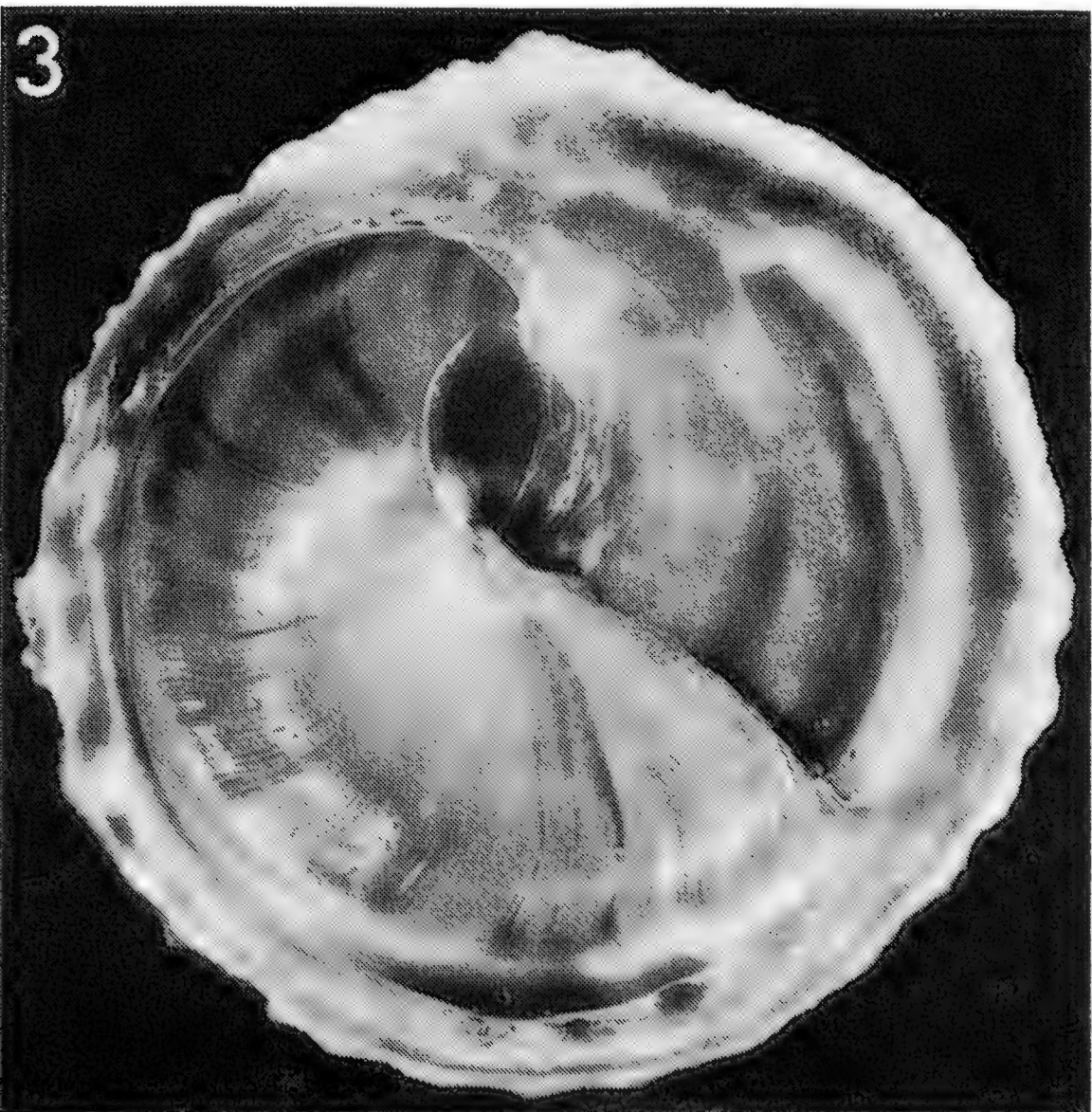
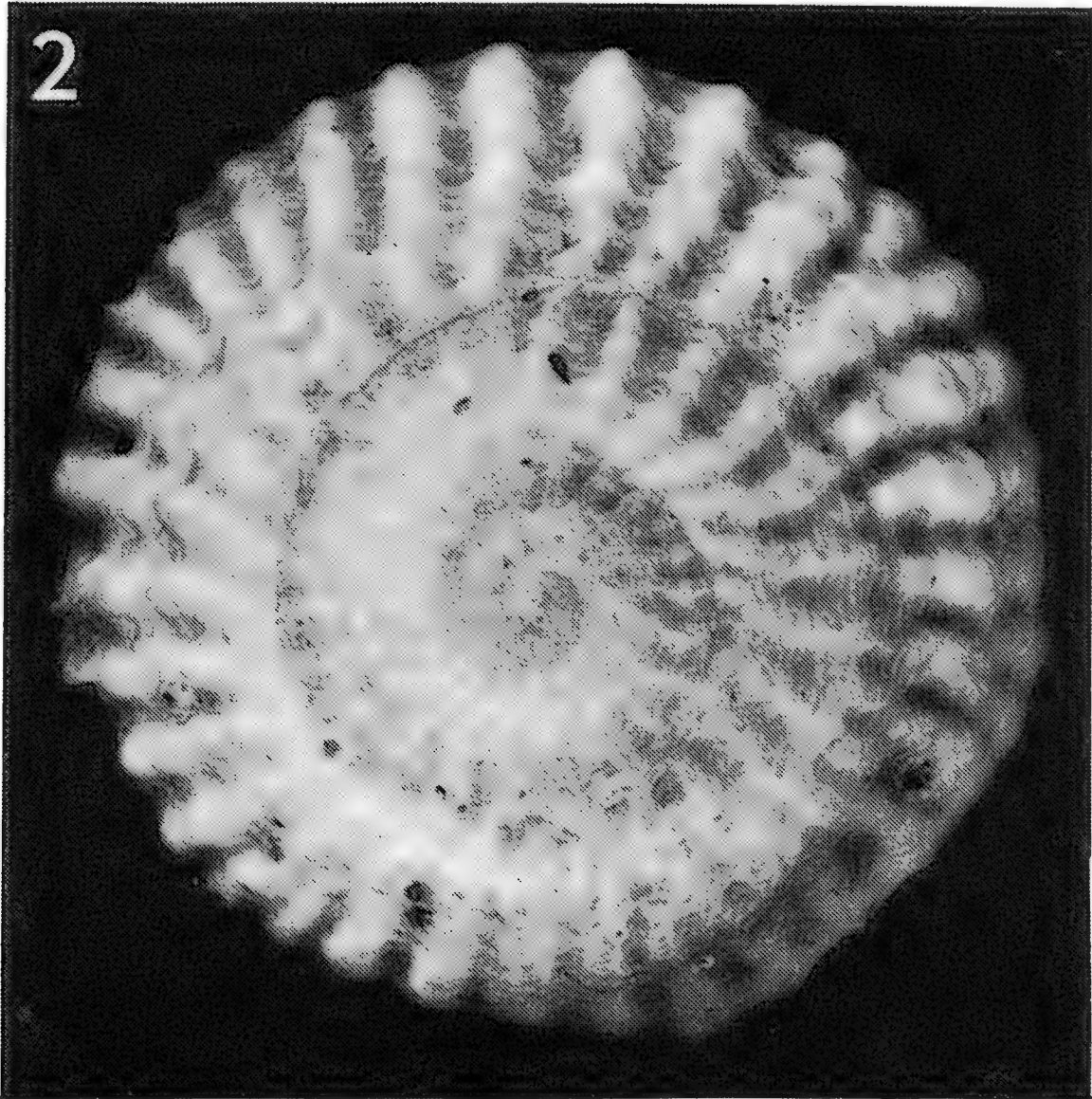
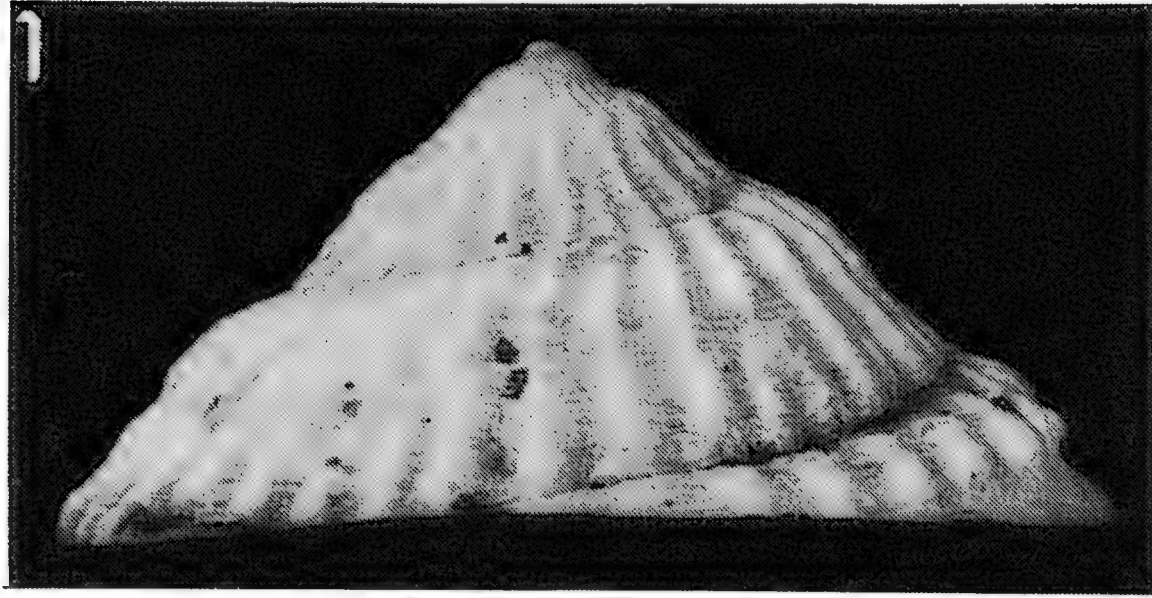
PLATE 6 (OPPOSITE)

*Trochita dhofarensis* Taylor & Smythe sp. nov., Holotype, B.M.N.H. Reg. No. 1984067.  
Fig. 1 lateral view, X 2; Fig. 2 apical view, X 2; Fig. 3 abapical view, X 2.

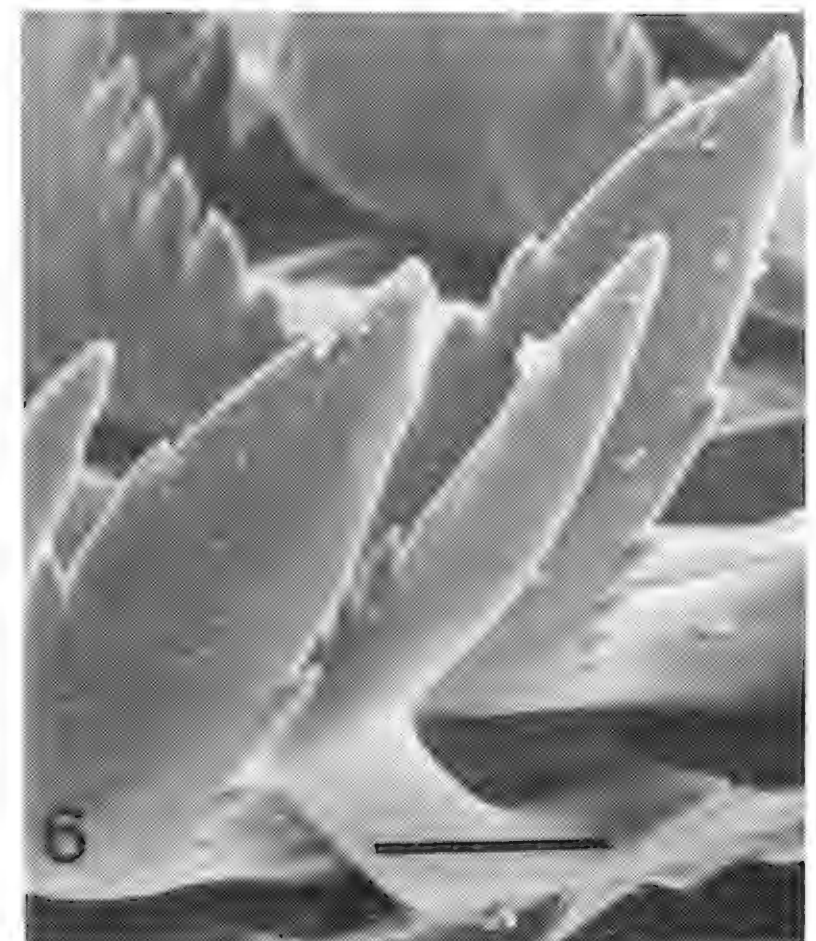
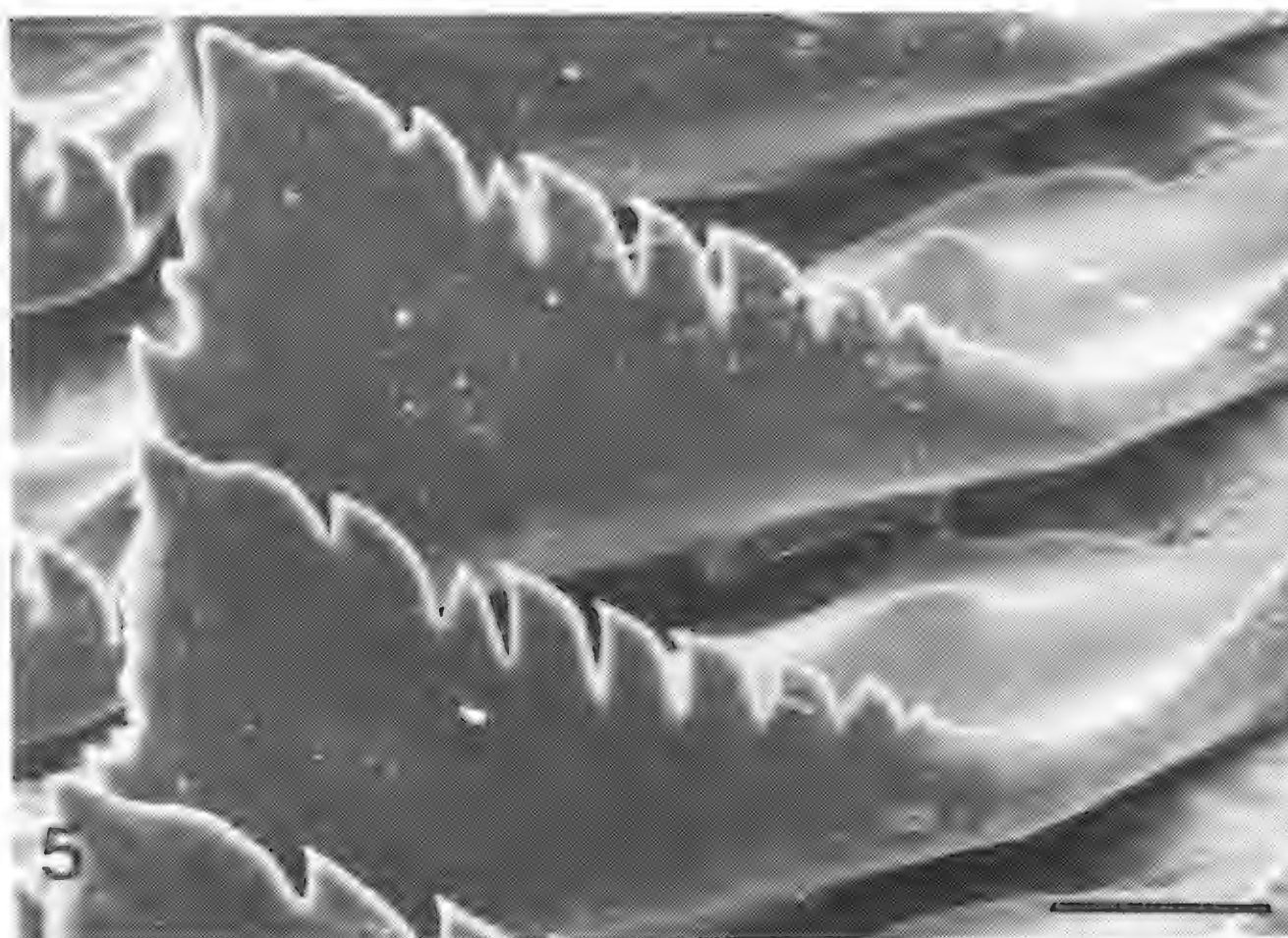
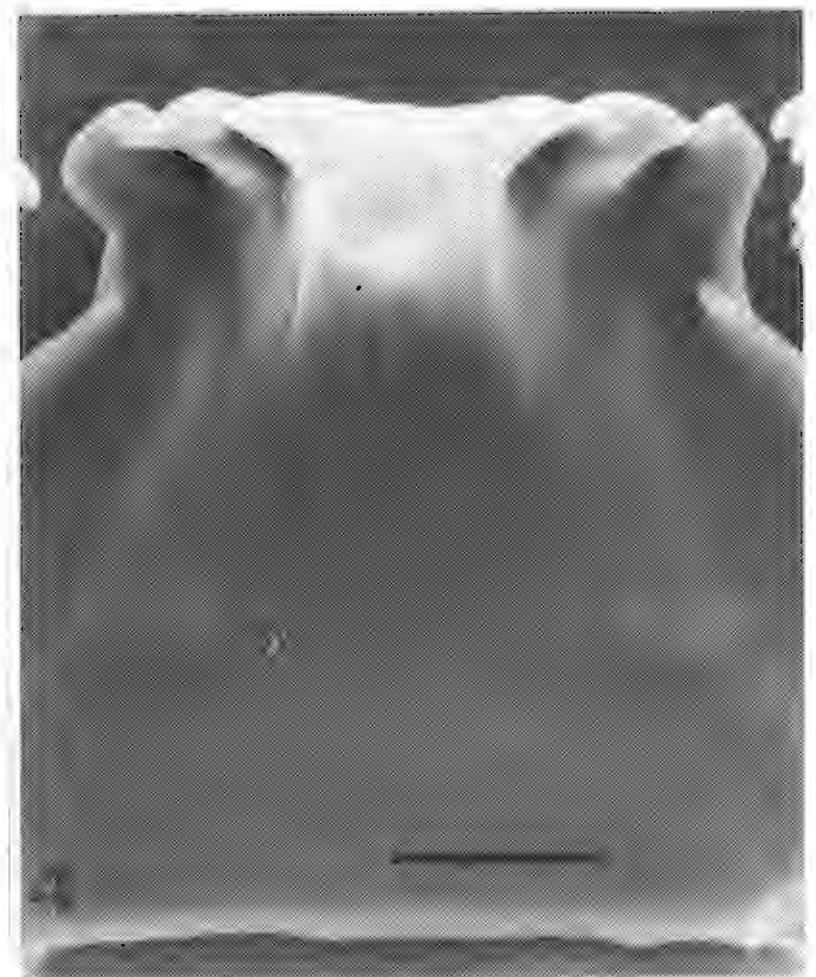
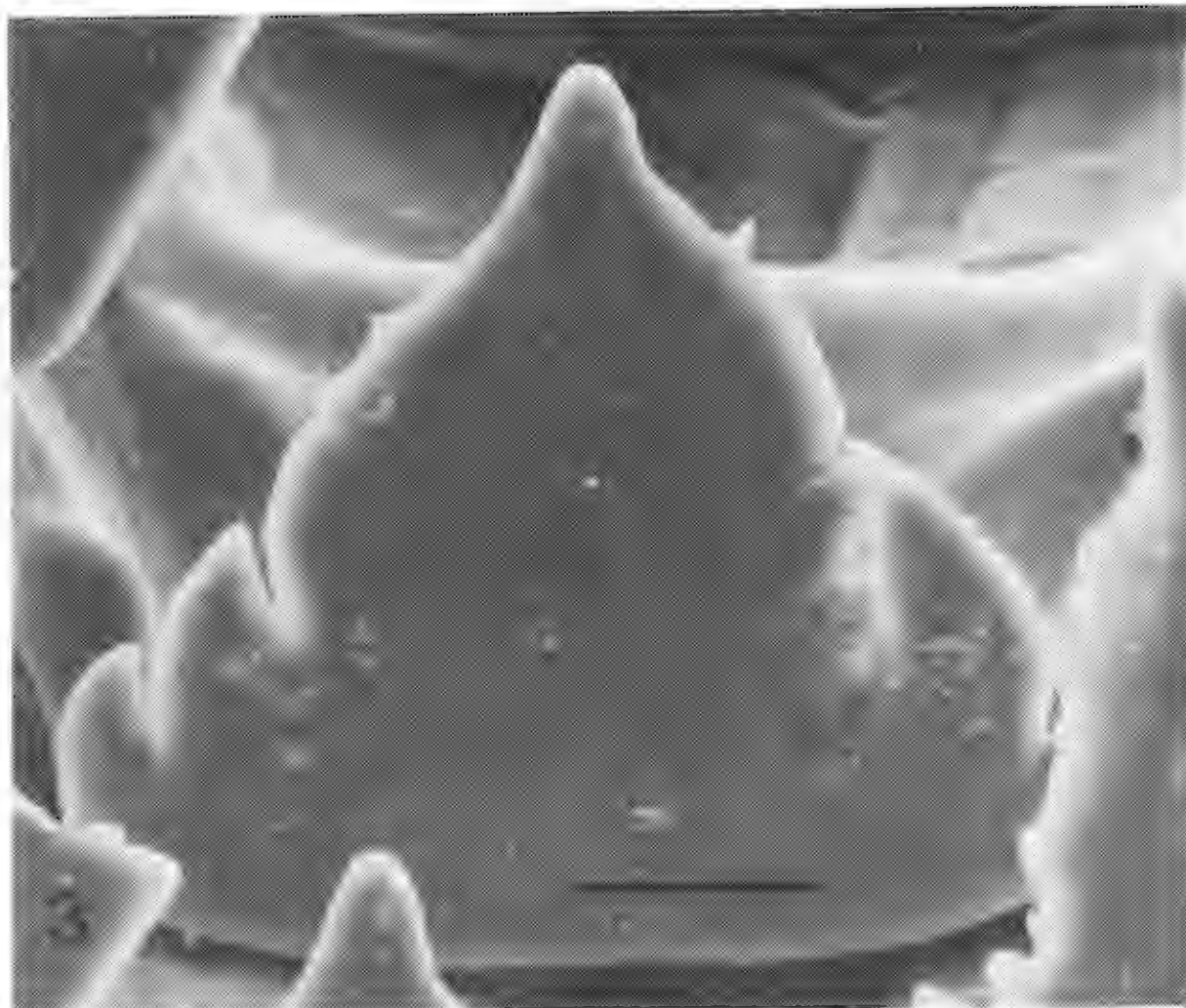
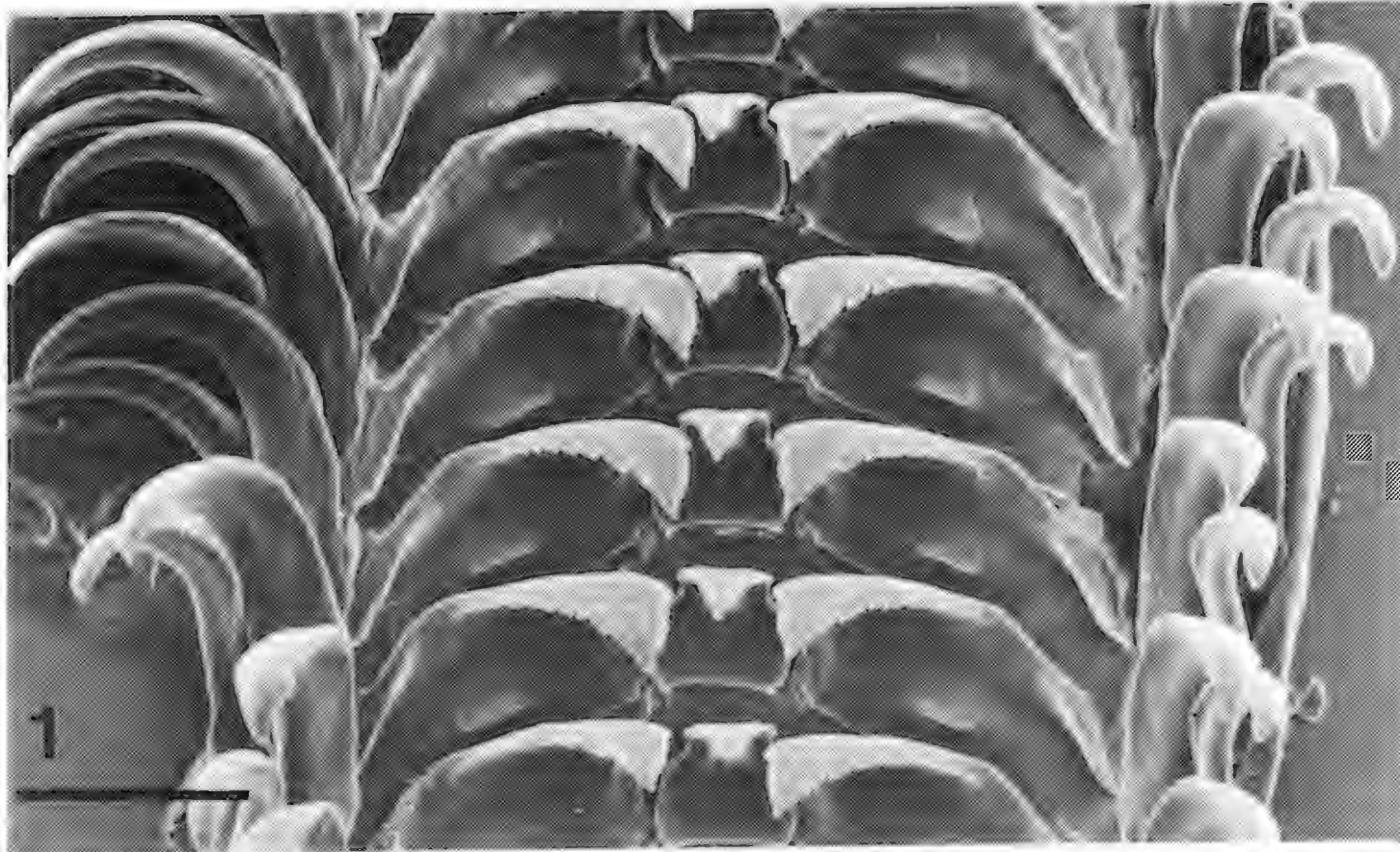
PLATE 7 (OVER LEAF)

Radula of *Trochita dhofarensis*

Fig. 1 general view of radula ribbon. Scale bar=100  $\mu\text{m}$ . Fig. 2 tips of marginal teeth. Scale bar=30  $\mu\text{m}$ . Fig. 3 central tooth from rear. Scale bar=10  $\mu\text{m}$ . Fig. 4 central tooth from front. Scale bar=10  $\mu\text{m}$ . Fig. 5 left lateral teeth from rear. Scale bar=30  $\mu\text{m}$ . Fig. 6 marginal teeth from side. Scale bar=30  $\mu\text{m}$ .









# INTRASPECIFIC VARIATION IN *NESOVITREA HAMMONIS* (STRÖM) (PULMONATA: ZONITIDAE) IN SWEDEN, WITH SPECIAL REFERENCE TO COLOUR DIMORPHISM<sup>1</sup>

TED VON PROSCHWITZ<sup>2</sup>

(Accepted for publication, 20 October 1984)

**Abstract:** Swedish *Nesovitrea hammonis* was investigated with regard to the distribution of a greenish-hyaline colour form (f. *viridula*); size of the shell ( $\emptyset_{maj.}$ ); and development of an internal rib (callus). Material from two localities surveyed every year 1970–82, and material from a great number of localities in SW. Sweden investigated 1920–22, and re-investigated 50 years later, showed a striking constancy in the relative number of f. *viridula*. This seems to be valid for localities apparently not affected by man, but the proportions were remarkably changed in localities severely influenced by human activities. The distribution of f. *viridula* seems to indicate a correlation with the maritime climate in SW. Sweden, where the form is common. Eastwards and northwards the frequency decreases rapidly and in northernmost Sweden f. *viridula* is absent. In the province of Dalsland the distribution of f. *viridula* was studied in more detail. Here the frequency of the form seems to decrease with decreasing annual precipitation. Shells from N. Sweden differ from those from SW. Sweden in two aspects; 1) the specimens reach a larger maximum size (a greater number of whorls) and 2) for each number of whorls the mean  $\emptyset_{maj.}$  is larger. The callus may be differently developed in material from various Swedish districts, often it is absent.

## INTRODUCTION

*Nesovitrea hammonis* (Ström) is a very common and eurotype species which is widely distributed throughout Western, Central and Northern Europe. Its total distribution is palearctic. Waldén (1966) discusses the variation of some characters within the species, mentioning that although some of the variation shows geographical correlation there is no reason for division into subspecies.

In some areas a light greenish-hyaline colour variant of *N. hammonis* [f. *viridula* (Menke)] occurs together with typical brownish specimens (f. *typica*). This greenish form was earlier often confused with the similar and closely related *N. petronella* (L. Pfeiffer), and the position of this as a distinct species was therefore questioned. The true relationships were clarified by Waldén (1966). The animal of *N. hammonis* is normally pigmented, which shows that f. *viridula* is not an albinotic form. The distribution of f. *viridula* shows a geographically correlated pattern (Waldén 1966), but this is only roughly known. In all probability f. *viridula* is genetically different from f. *typica*, and the distribution pattern indicates a connection with certain environmental factors.

Material collected in Sweden, Denmark and Norway by H. Lohmander and H. W. Waldén, during the faunistic research programme of the Göteborg Natural History Museum (Waldén 1965) is very useful for studying variation in different characters because of the large samples from numerous localities.

<sup>1</sup> This is an extended version of a lecture held at the 8th International Malacological Congress in Budapest 1983.

<sup>2</sup> Natural History Museum, Box 7283, S-40235 Göteborg, Sweden.

This paper intends to show, in detail, the distribution of the two colour forms in the province of Dalsland, SW. Sweden and to discuss the possible correlation with environmental factors. The distribution in other, more superficially studied areas in SW. Sweden, is also discussed. These results are compared with the distribution pattern throughout Scandinavia. In addition, the relative proportions of f. *typica* to f. *viridula* have been studied at two localities over a long term of years. The same relation has also been studied on localities surveyed with great time intervals (up to 50 years and more).

Little is known about variation in size of the shell between populations of *N. hammonis* from different areas. However, Waldén (1966) stated that specimens from northern Sweden reach larger dimensions than those from southern Sweden. In this study four series of shells from southern Sweden (two from the same series of localities, investigated after an interval of 50 years) were compared with each other and with material from northern Sweden with regard to the largest diameter  $\emptyset_{\text{maj.}}$ .

A third character, which varies considerably between populations of the species from different parts of Sweden, is the formation of an internal rib (callus) in the aperture. The known facts are briefly discussed, but in this case the knowledge is still very incomplete.

#### METHODS

Shells used in this study are from the collections of the Natural History Museum, Göteborg, collected by H. Lohmander, H. W. Waldén and myself. Localities (Fig. 1) and years of collection were as follows:

1)+2)	The vicinity of Göteborg	1921–22, 1971–78
3)	The central parts of the province of Västergötland	1925
4)	The province of Dalsland	1938–57, 1964–67, 1975–82
5)	The western parts of Lycksele lappmark	1961–63

Two series were used to study the proportions between the two colour forms over a long period:

6)	Stora Mollungen—province of Västergötland	1970–81
7)	Hamra—province of Halland	1970–82

The proportions between f. *typica* and f. *viridula* in different areas were calculated by using the locality quotient. This is the number of localities with f. *typica*/number of localities with f. *viridula*. In one case the abundance-quotient, which is the total number of f. *typica* specimens/total number of f. *viridula* specimens, was calculated. Relative distribution figures, calculated as means of the percentage distribution of the colour forms in each of the 82 samples from the vicinity of Göteborg were also used.

About 100 specimens from each area were measured ( $\emptyset_{\text{maj.}}$ ) and the number of whorls was determined according to Ehrmann (1933). Linear regression with  $\emptyset_{\text{maj.}}$  (=y) as a function of the number of whorls (=x) was performed.  $\chi^2$ - and t-tests were used to calculate differences. A difference was regarded as significant if  $p < 1\%$ , probably significant if  $1 < p < 5\%$  and not significant if  $p > 5\%$ .

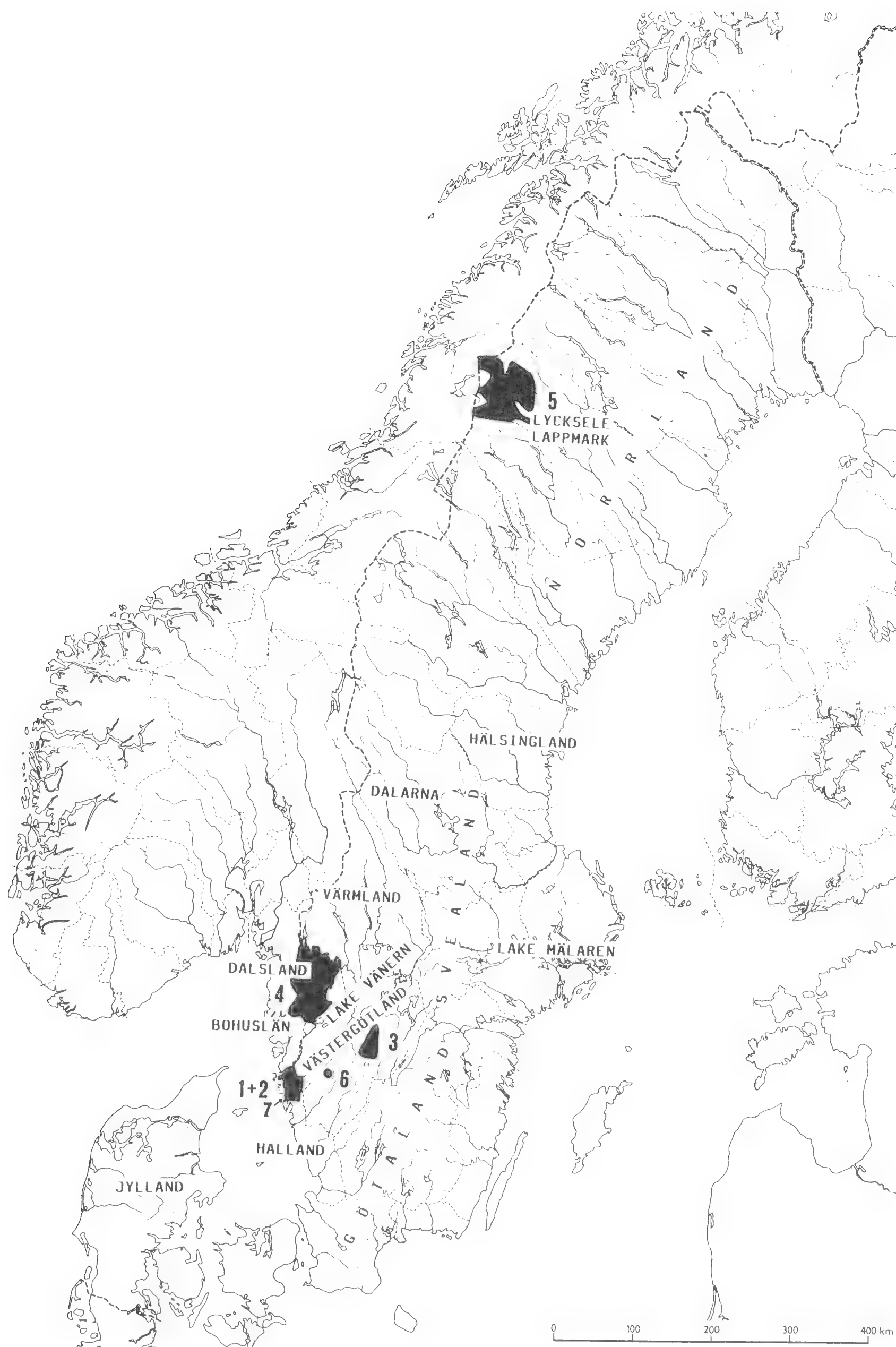


Fig. 1. Map showing the position of the investigated areas and localities. 1+2. The vicinity of Göteborg. 3. The central parts of the province of Västergötland. 4. The province of Dalsland. 5. The western parts of Lycksele lappmark. 6. The special locality St. Mollungen. 7. The special locality Hamra.



## RESULTS

*Colour dimorphism*

Constancy of the character: Samples collected once a year from two localities, Stora Mollungen and Hamra, in SW. Sweden over a period of 12 and 13 years were studied with respect to number of specimens of *f. typica* and *f. viridula*. The collections were made at approximately the same time every year (end of May to the beginning of June). Sampling was carried out by sifting litter using the same method as in the faunistic research programme (Waldén 1965). The total number of specimens fluctuated considerably, but the relative proportion of the colour forms remained strikingly constant over the whole period (Figs. 2–5). The greatest deviations (17%) were between 1978 and 1974, between 1978 and 1975 and between 1978 and 1982 in the Hamra series. In the Stora Mollungen series the years 1975 and 1976 differed the most (22%). The homogeneity of both series was tested with contingency-table  $\chi^2$ -tests. These showed no significant differences.

Shells collected from a series of localities in the vicinity of Göteborg during 1921–22 and 1971–78 were used to study changes within each locality and for the whole area. The frequency and abundance of *f. typica* and *f. viridula* in these samples are shown in Tables 1 and 2. The locality quotients show that *f. typica* is slightly more common within the area. The number of localities for both forms were also approximately the same in both date classes—the small differences were not significant. However, for the total number of specimens *f. typica* was dominant (Table 2). The abundance quotients give the impression of a regression of *f. viridula* and a  $\chi^2$ -test of the total number of specimens showed a significant difference. When single samples were studied, however, a few very large samples showed considerable differences in the proportions between the forms. These large samples may have caused considerable bias in the results. To avoid this the percentage figures were calculated for each of the samples and, based on these, the means for the whole set (Table 2). These figures are independent of the number of specimens in the sample. When t-tested they showed no significant difference. For the whole area the proportions between the forms must therefore be considered as relatively constant. However, when examined on an individual basis, some samples showed considerable differences in the proportions of the two forms in the two date classes. 19 of the 82 localities investigated exhibited a marked alteration (>30%), 26 showed a moderate alteration (16–30%) and 37 showed little or no alteration (0–15%). There was no consistent trend in the alterations. Thus 36 samples showed an increase in *f. typica* and 39 an increase in *f. viridula*. The Göteborg-district has undergone considerable changes since the 1920s because of increased urbanisation and industrialisation. Some of Lohmander's localities have been destroyed and many heavily disturbed by human activity. The localities with large alterations in the proportions between *f. typica* and *f. viridula*, and some with moderate alteration, were those which had been severely disturbed by man. In Dalsland, 6 localities visited by Lohmander (4 in 1938 and 2 in 1957) were reinvestigated in 1982. The conditions for 3 of these localities seemed to have remained relatively unchanged and samples from them showed only small deviations from the earlier findings. However, the other 3 localities had been severely damaged by human activity such as cutting and planting of spruce, and there were considerable changes in the proportions between *f. typica* and *f. viridula*.

*Geographical variation*

Frequencies in the studied areas are presented in Table 1. In the vicinity of Göteborg *f. typica* and *f. viridula* occurred in approximately the same number of localities, usually

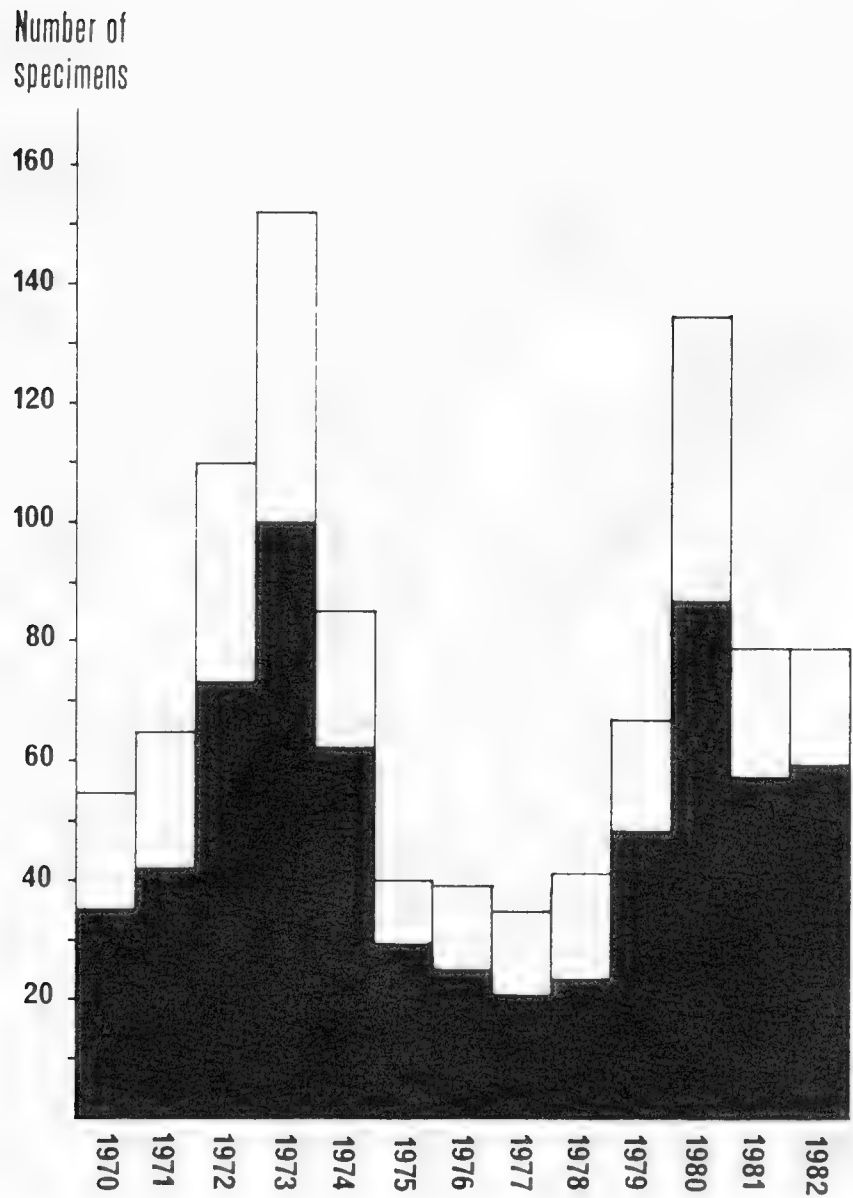


Fig. 2. Number of specimens of *N. hammonis* in samples from Hamra 1970-82. Black: f. *typica*, white: f. *viridula*.

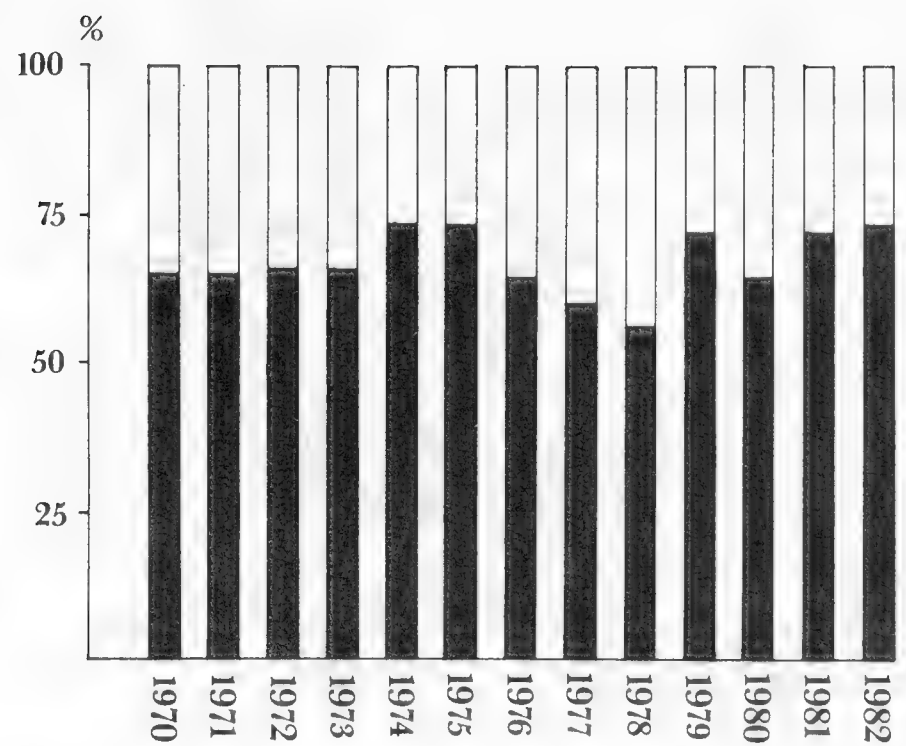


Fig. 3. Percentage of f. *typica* (black) and f. *viridula* (white) in samples of *N. hammonis* from Hamra 1970-82.

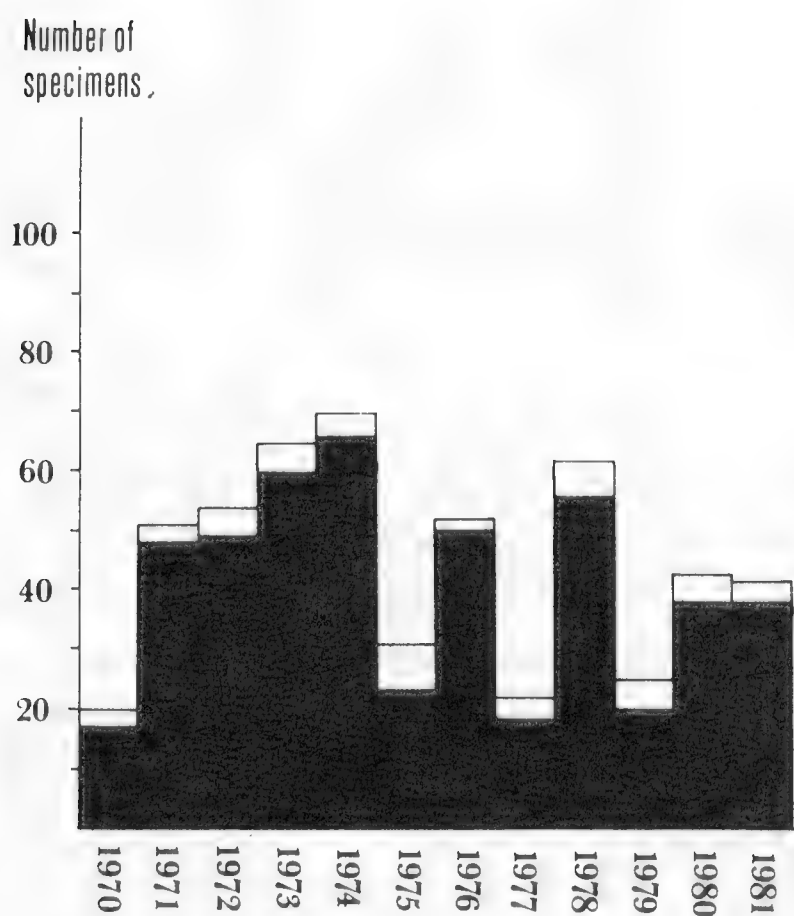


Fig. 4. Number of specimens of *N. hammonis* in samples from St. Mollungen 1970-81. Black: f. *typica*, white: f. *viridula*.

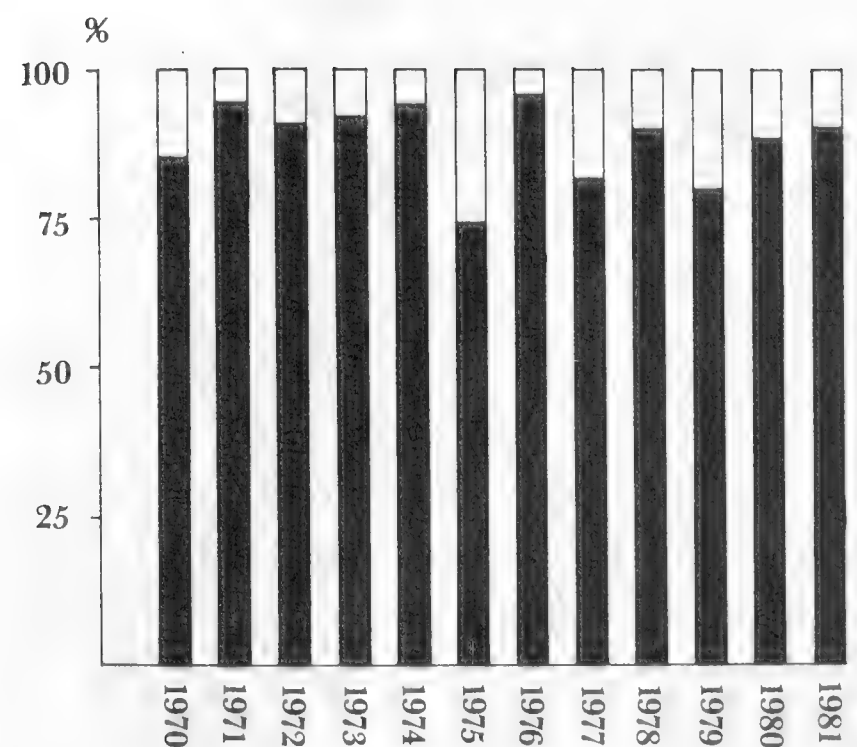


Fig. 5. Percentage of f. *typica* (black) and f. *viridula* (white) in samples of *N. hammonis* from St. Mollungen 1970-81.

TABLE 1

Frequencies of the colour forms of *N. hammonis* in different districts of Sweden.

District	Number of localities	% of localities with:		Locality-quotient
		f. <i>typica</i>	f. <i>viridula</i>	
The vicinity of Göteborg 1921–22	82	98	79	1,25
The vicinity of Göteborg 1971–78	82	96	85	1,13
The central parts of the province of Västergötland 1925	45	96	11	8,60
The province of Dalsland 1938–57, 1964–67 and 1975–83				
a) Totally:	661	99	24	4,20
b) Divided into following precipitation areas (fig. 7):				
>800 mm/year	175	99	33	3,00
800–750 mm/year	301	99	27	3,68
750–650 mm/year	150	99	12	8,22
<650 mm/year	35	100	3	35,00

In the vicinity of Göteborg only material from 82 localities with the sampling sites located in exactly the same place in the 1920s and the 1970s has been used. In Dalsland and central Västergötland material from all surveyed localities was used.

TABLE 2

Abundance and relative distribution in single samples of the colour forms of *N. hammonis* from the same localities in the vicinity of Göteborg 1921–22 and 1971–78.

District	Abundance			Relative distribution in single samples			
	Number of specimens:	Abundance-				$S_x$	$S_{\bar{x}}$
	f. <i>typica</i>	f. <i>viridula</i>	quotient	$\bar{x}$ <i>typica</i>	$\bar{x}$ <i>viridula</i>	(S.D.)	(S.E.)
The vicinity of Göteborg 1921–22	1172	594	1,97	0,666	0,334	0,2666	0,0294
The vicinity of Göteborg 1971–78	1692	709	2,39	0,685	0,315	0,2600	0,0287

Material from the same 82 localities as in Table 1. The relative distribution figures have been calculated as a mean of the percentage distribution of the colour forms in each of the 82 samples.

together. In central Västergötland f. *viridula* is much rarer. In Dalsland, as a whole, f. *typica* dominates but f. *viridula* is rather common (Fig. 6). The picture is somewhat complicated, but a decrease in the number of localities with f. *viridula*, going from west to east can be noted. This decrease coincides approximately with the decrease in precipitation which is clearly marked in the same direction within the province (cf. precipitation areas in Fig. 6 with the frequency values in Table 1). In Fig. 7 the frequencies of the two forms in the different precipitation areas are presented as circle sectors. This clearly illustrates the decrease of f. *viridula* with decreasing precipitation.  $\chi^2$ -tests showed a significant difference between the 800–750 mm and the 750–650 mm areas, and a probably significant difference between the 750–650 mm and the <650 mm areas. The difference between the >800 mm and the 800–750 mm areas was not significant.



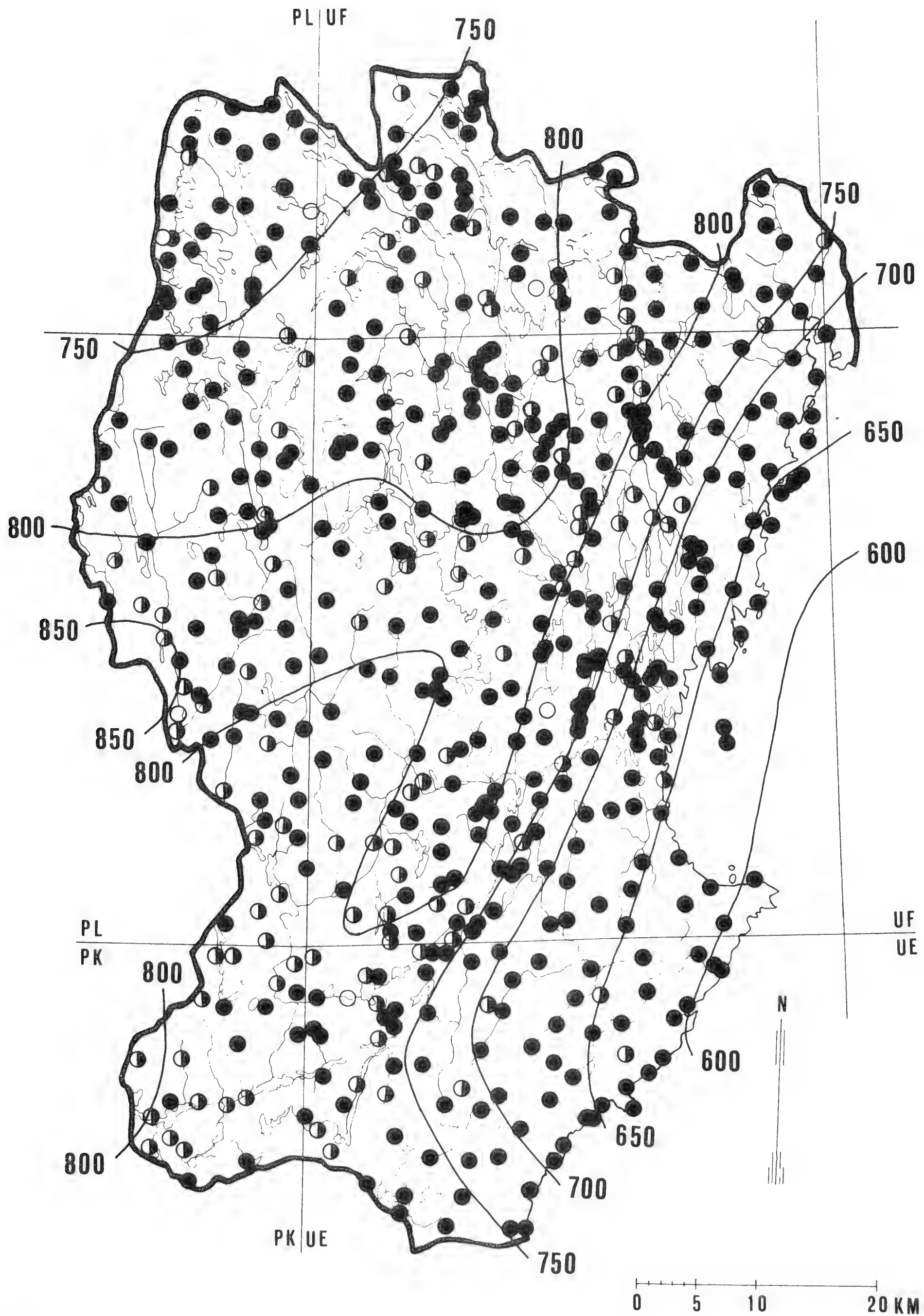


Fig. 6. Distribution of the colour forms of *N. hammonis* in Dalsland.

● *f. typica*    ◐ *f. typica+f. viridula*    ○ *f. viridula*.

Lines connect sites with the same annual precipitation.

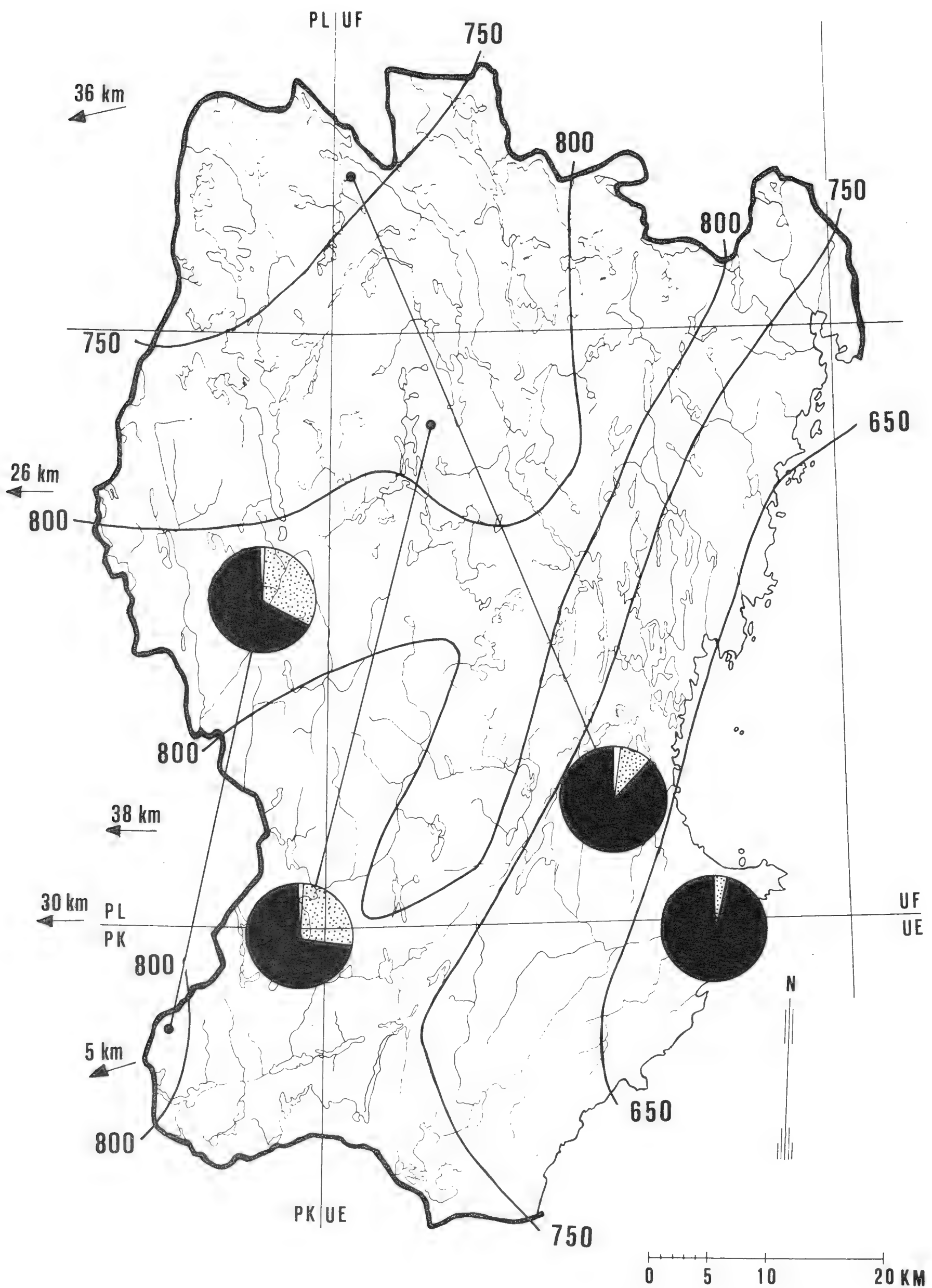


Fig. 7. Relative frequencies of localities with the different colour forms of *N. hammonis* indicated as circle sectors in different precipitation areas of Dalsland. The lines connect sites with the same annual precipitation. Black sector of circles=percentage localities with *f. typica* only.

Dotted sector of circles=percentage localities with *f. typica* and *f. viridula*.

White sector of circles=percentage localities with *f. viridula* only.

Arrows with figures in the left of the figure indicate direction and distance to the sea from the western border of the province.

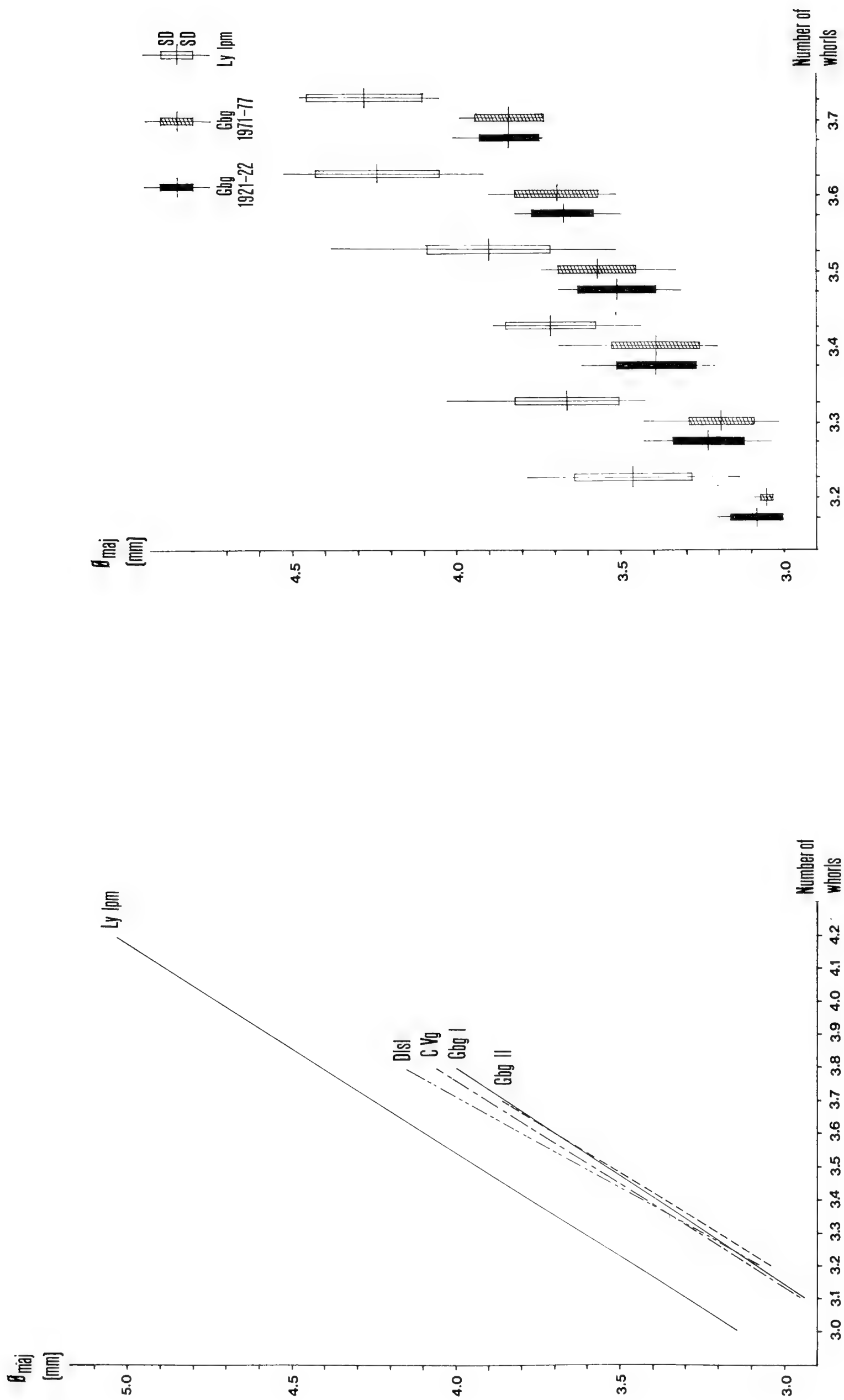


Fig. 8. Linear correlations between size ( $\varnothing_{maj}$ ) the number of whorls in *N. hammonis* in 5 different sets of material from Sweden. Gbg I=The vicinity of Göteborg 1921-22 ( $y=1.52x-1.78$ ). Gbg II=The vicinity of Göteborg 1971-77 ( $y=1.63x-2.18$ ). C. Vg.=The central parts of the province of Västergötland 1925 ( $y=1.58x-1.95$ ). DlsI.=The province of Dalsland 1978-80 ( $y=1.81x-2.72$ ). Ly. lpm.=The western parts of Lycksele lappmark 1961-63 ( $y=1.58x-1.59$ ).

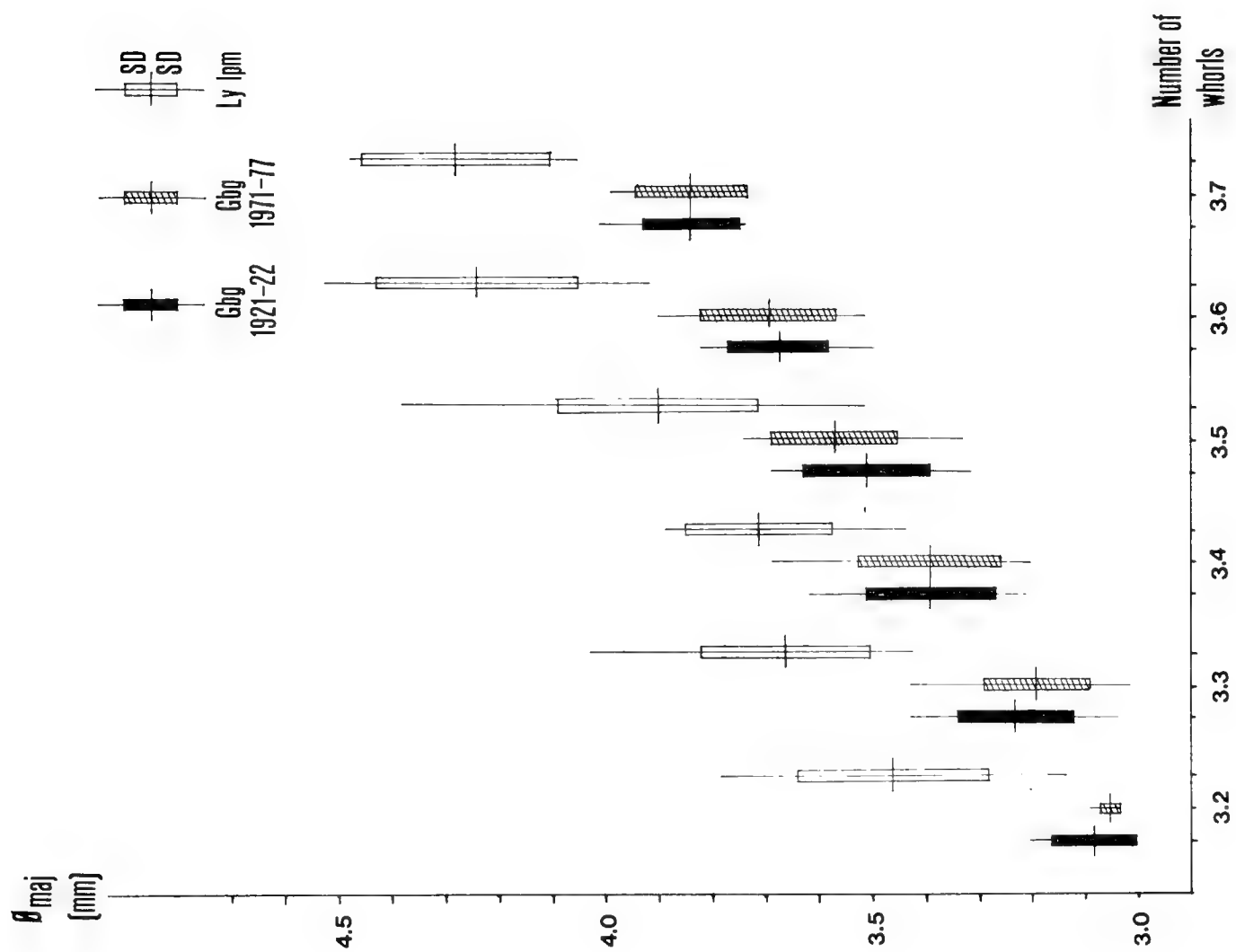


Fig. 9. Variation in  $\varnothing_{maj}$  at different numbers of whorls in *N. hammonis* in 3 sets of material from Sweden. See Fig. 8 for abbreviations.



*Size of the shell*

The linear correlations between  $\emptyset_{\text{maj.}}$  and number of whorls in the five sets of material are presented in Fig. 8. In the four S. Swedish sets the correlations are very similar. Fig. 9 shows the variation in  $\emptyset_{\text{maj.}}$  at different numbers of whorls in three sets of shells. The two sets from the Göteborg district—collected on the same localities after an interval of about fifty years—were compared using t-tests. No significant differences were found between the Göteborg material or between any of the four S. Swedish sets of material. The shells from Lycksele lappmark, however, differ significantly (except in one case,  $\emptyset_{\text{maj.}}$  at 3.7 whorls) from those from southern Sweden.

The results indicate that the species in northern Sweden becomes larger than in southern Sweden in two respects:

- 1) the specimens reach a larger maximum size (a greater number of whorls)
- 2) for a certain number of whorls the mean  $\emptyset_{\text{maj.}}$  is larger than in the S. Swedish material.

*Formation of callus*

An internal rib in the aperture (callus) occurred in the material from Dalsland and the vicinity of Göteborg but not in that from central Västergötland. The character can only be studied in adult specimens, and the samples were too small for statistical treatment. However, in the Göteborg material the callus was rather rare but when it occurred it was often very well developed, sometimes even showing a tendency to divide into separate teeth. In the material from Dalsland the callus was more common but usually it was relatively weak and never so well developed as in the shells from the vicinity of Göteborg.

## DISCUSSION

*Colour dimorphism*

Constancy of the character: The Hamra- and St. Mollungen-series provide strong evidence for constancy in the proportions between f. *typica* and f. *viridula* over a long time period (Figs. 3 and 5). (cf. The study of Goodhart (1973) concerning constancy of colour forms in populations of *Cepaea nemoralis*). Fig. 2 suggests, improbably, that the samples reflect cyclical changes in the population size over the years. The St. Mollungen series also showed changes but these were smaller and did not seem to follow any pattern (cf. also Mason (1970), who did not find any type of regular variation in populations of litter-living snails). Fluctuations may be due to a period of drought some time before the samples were collected. It is always more difficult to obtain molluscs by sifting of litter after long drought.

When comparing the sets of material from the vicinity of Göteborg the question of constancy becomes more complicated. As mentioned, increased urbanisation and industrialisation have strongly altered this area since the 1920s. The locality quotients (Table 1) do not differ significantly. The relative distribution of the forms in single samples (Table 2) is also very similar. This, however, is valid only for the area as a whole. Some of the single samples showed considerable changes in the proportion over the period. The difference in the total number of specimens of the two forms, which showed a reduction in f. *viridula* was due to such changes in a few very large samples. The changed proportions may be due to different factors:

- 1) Even if the localities surveyed by Lohmander in 1921–22 have been localised exactly, the samples may not have been taken in exactly the same site of the habitat.
- 2) Many of the localities have been affected by human activities, some markedly so. Changes in the proportions between the forms may take place in different ways: A) It is possible that the forms differ in sensitivity to changes in the habitat. Waldén (1966) postulates that f. *viridula* may be slightly more stenoecious than f. *typica* but no such tendency could be traced in the material. B) If the locality becomes severely disturbed by such activities as trampling, cutting and planting of spruce, it is probable that large parts of the population would have been wiped out. This may alter the gene pool in such a way that one of the colour forms becomes rare or disappears (drift effects).

It is notable that the localities which showed the largest changes were all severely disturbed. The seemingly unchanged localities showed, in the vast majority of cases, good conformity between the samples and the results from the reinvestigated localities in Dalsland confirm what has been stated above about the forms in the vicinity of Göteborg. Thus there is strong evidence for constancy in the proportions between f. *typica* and f. *viridula* in a population over long time periods as long as the habitat is relatively unaltered.

### *Geographical variation*

The preliminary results from the collections by Lohmander and Waldén in Sweden, Denmark and Norway provide an approximate picture of the distribution of f. *viridula*. It will be briefly outlined here and the results from SW. Sweden will be discussed with this general picture as a background. In southern Sweden (Götaland) f. *viridula* is known from all districts but in very different frequencies of occurrence. In SW. Sweden f. *viridula* is very common. Eastwards the frequency decreases considerably. In large areas of central and eastern Götaland the form is very rare or even absent, although locally it may appear rather abundant. In Svealand it is not uncommon in southern Värmland. In the northern parts of this province it becomes rarer. In the eastern parts it seems to diminish in the region of Lake Mälaren. North of these areas only a few records are known; one from eastern Dalarna and one from Hälsingland. From the upper parts of Norrland it is not known at all. In Denmark f. *viridula* is widespread on Jylland (Lohmander 1959). It is also common in western Norway, but seems to be missing in the eastern and northern parts of the country. Outside Scandinavia f. *viridula* occurs on the British Isles but not on Iceland (Waldén 1966). The form occurs on the European continent but its distribution is still very incompletely known.

The results from the present study agree closely with the general picture described above. The high frequencies of f. *viridula* in SW. Sweden and W. Norway, together with the low frequencies in the middle and eastern parts of S. Sweden and its total absence in upper Norrland, indicate a connection with suboceanic conditions and a maritime climate. The absence of f. *viridula* in the coastal parts of northern Norway and on Iceland seems to be contradictory, but in these areas other factors may be of crucial importance. One such factor may be origin of the populations which first colonised the areas.

In Dalsland the decrease in f. *viridula* with decreasing precipitation in the west-east direction is clearly marked. The province represents, with respect to precipitation, a transition between a western maritime climate and a dryer middle Swedish inland climate (Andersson 1981). In this context it may be worth noting the distance to the sea in different parts of the province. From the SW. corner the distance to the deep penetrating fiord Gullmarsfjorden is only 5 km. In the middle and northern parts, however, there are no penetrating fiords and the distance from the border to the coast is between 25 and 40 km. The areas in eastern Dalsland with lower precipitation are about 70–85 km away from the

sea (cf. Fig. 7). In spite of the relatively short distances within the province the difference in precipitation between the western and eastern parts is more than 250 mm/year. The maritime climate in the western parts, due to the relatively short distance to the sea and the exposure to depressions coming in from the Atlantic, is influenced by topography. The uplands in western Dalsland force the damp air masses upwards and this causes powerful orographic precipitation (cf. Fig. 6). In this context humidity (the part of the precipitation which does not evaporate) must also be considered. According to Tamm (1959) and Ångström (1968) the humidity agrees fairly well with the distribution of the precipitation within the province. However, the situation is somewhat different when temperature is considered. The eastern parts of the province, adjacent to Lake Vänern, has a temperature typical of a maritime climate. This is due to the large water mass, which causes a temperature equalisation (Andersson 1981). The contrast between precipitation- and temperature-climate is similar to the situation in the outer costal region of the province of Bohuslän. Frequency figures from different parts of this province may therefore throw more light on the possible influence of interacting climatological factors on the colour forms of *N. hammonis*.

Boycott (1934) characterises *N. hammonis* as a species with a very wide ecological range. Waldén (1966) confirms this and the species is without doubt the most abundant landsnail in Sweden (cf. Mordan 1977 for conditions in Britain). Very little is known about differences in the ecology of the colour forms. Lohmander (1959) stated that f. *viridula* in western Jylland in Denmark seems to prefer drier habitats. However, in SW. Sweden f. *viridula* is often found in different kinds of marshes. Waldén (1966) remarks that f. *viridula* may be slightly more stenoecious. My results from Dalsland seem to confirm that there is no difference in the ecology. There did not seem to be any connection between the occurrence of f. *viridula* and the degree of insolation at the locality, although this was not tested statistically.

The underlying causes for the connection of f. *viridula* to maritime climate in SW. Scandinavia remain unclear, although precipitation and maybe also other climatological factors are of importance. When more definite results concerning the distribution and frequency of f. *viridula* over the whole S. Scandinavia are available, a detailed analysis will throw more light on this complex of problems. Laboratory tests of the reactions of the forms to difference environmental factors are also necessary.

### *Size of the shell*

Some terrestrial snail species, with a wide geographical distribution, reach a larger size in northern latitudes. This is true for both *N. hammonis* and the closely related *N. petronella* (Waldén 1966). Up to now, however, larger size has been associated only with a greater number of whorls. This is indeed true, but for the material from Swedish Lappland the mean  $\bar{\varnothing}_{\text{maj.}}$  for a certain number of whorls is also larger (Figs. 8, 9). Studies of more shells will show if this has general validity. As the geographical distance between the northern and the three southern studied areas (which lie rather close to each other) is considerable, it is also desirable to study material from the intermediate areas. These studies could reveal important information on the, probably clinal, transition in size of the shell in terms of the number of whorls and  $\bar{\varnothing}_{\text{maj.}}$  for a certain number of whorls. The material from the vicinity of Göteborg (Fig. 9) showed that  $\bar{\varnothing}_{\text{maj.}}$  varied very little over a long period of years. Both characters are probably largely controlled by genetical factors while environmental influence is probably of minor importance (cf. Waldén 1966).



### *Formation of callus*

This character must have a genetic background, but nothing is known of possible constancy over generations in a population or the possible influence of environmental factors. However, the callus is differently developed in shells from different districts and it is possible that further research may reveal geographically correlated patterns. Calcium availability may be important since it is required in the formation of the callus. In the material from central Västergötland, which is rich in lime, the callus was not, however, observed. In the material from Dalsland, which is lime-rich in some areas, a moderately developed callus occurred rather frequently. It may also be mentioned that specimens sampled from wetland habitats in Dalsland seemed to lack a callus completely, although this was not tested statistically. Another way of testing the influence of humidity upon the formation of callus could be comparison of materials from dry and rainy seasons.

### ACKNOWLEDGEMENTS

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# AN UNDESCRIBED *ACICULA* (GASTROPODA: ACICULIDAE) FROM PORTUGAL AND A RECORD OF *A. ALGERENSIS* IN MOROCCO

D. T. HOLYOAK<sup>1</sup> AND MARY B. SEDDON<sup>1</sup>

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*Abstract:* *Acicula lusitanica* sp. nov. is described from south-western Portugal. *Acicula algerensis* Gittenberger & Boeters is reported from north-western Morocco.

## INTRODUCTION

The small prosobranch land snails of the family Aciculidae are widespread in the western Palaearctic Region, but uncommon and of local occurrence in the Iberian Peninsula and north Africa. During August 1984 species of *Acicula* were collected by the authors and Mr. M. Holyoak in NW. Morocco and SW. Portugal. These finds represent the first records of the genus from each of these countries. The Portuguese form shows a combination of characters sufficiently different from those of known species for its description as a new species to be justified. The Moroccan specimens resemble *Acicula algerensis* Gittenberger & Boeters 1977 which was hitherto known only from five shells from Algeria. The family Aciculidae as a whole was reviewed by Ehrmann (1908), Kobelt (1908) and Hesse (1920). Gittenberger & Boeters (1977) revised Algerian records of *Acicula* s. str. and described *A. algerensis* and *A. norrisi* as new species from Algeria and Gibraltar respectively; Kerney, Cameron & Jungbluth (1983) described and figured all of the western and central European Aciculidae; Holyoak & Seddon (1985) gave several distributional records from northern Spain.

## ***Acicula lusitanica* sp. nov. (Plate 8)**

### *Description*

The small and slender shell has 5–6 whorls that enlarge slowly and regularly to give a very narrowly conical outline interrupted by the distinct suture. The surface is smooth and glossy, marked by very weak radial lines of growth (a few stronger radial growth-lines are also present on most shells). The fresh shell is translucent with the apical one or two whorls of the spire almost colourless; later whorls are light brown. The aperture is oval-pyriform. The peristome is simple and unthickened on the palatal margin, slightly thickened and narrowly reflected on the columellar margin. The palatal margin of the aperture is almost straight when viewed from the side and obliquely truncated. The peristome forms a rather sharp angle between the columellar and lower palatal borders of the aperture. The aperture lacks an upper palatal sinulus and does not show other peculiarities.

<sup>1</sup> Department of Geography, University of Nottingham, Nottingham NG7 2RD.



*Measurements*

Holotype height 3.0 mm, breadth 1.0 mm; paratypes 2.6–3.5×0.9–1.0 mm.

*Comparisons*

The genus *Acicula* has usually been divided into three subgenera, *Acicula* s.s., *Hyalacme* and *Platyla*. *A. lusitanica* differs from species of subgenus *Acicula* s.s. in lacking strong incised radial lines on the shell. *Acicula (Hyalacme) diluviana* (Hocker), known only from European Pleistocene deposits, differs in possessing an upper palatal sinulus. That species and the east European *A. (H.) perpusilla* (Reinhardt) also differ in having the palatal margin of the aperture parallel to the long axis of the shell, not obliquely truncated as in *A. lusitanica*.

The smooth shell and moderately deep suture of *A. lusitanica* suggest subgenus *Platyla* Moquin-Tandon 1855. However, *A. lusitanica* differs from all western and central European species (*A. polita* (Hartmann), *A. gracilis* (Clessin), *A. cryptomena* (Folin & Bérillon), *A. callostoma* (Clessin), *A. dupuyi* (Paladilhe)) in the following characters: shell apex narrower, with whorls more tightly coiled and tapering more gradually; palatal sinulus absent; absence of thickening outside the palatal edge of the peristome. Because *A. lusitanica* lacks the features of the shell aperture that characterise subgenus *Platyla* caution is needed in assigning it to this group. However, this lack of distinctive features offers an insufficient basis for introduction of a new subgeneric name, especially as the genus as a whole is in need of taxonomic revision using characters additional to those of the shell.

*Type Locality*

Limestone crag on hill W. of N120 road at  $\frac{1}{2}$  km SSE. of church at Bensafrim, Distrito Faro, Portugal; c. 50 m ASL; UTM square NB21.

Material: Besides the Holotype (lodged in National Museum of Wales, Cardiff as NMWZ 1984.88), 60 paratypes from the same locality.

Derivatio nominis: living in Portugal.

*ACICULA (ACICULA) ALGERENSIS* GITTENBERGER & BOETERS 1977

Nine shells of *Acicula* collected from a rocky limestone hillside at N. edge of Chechaouèn, Morocco at c. 620 m ASL are a good match for this species, which was hitherto known only from northern Algeria (Gittenberger & Boeters 1977).

The two smallest of the four intact adult shells (3.3×1.3 and 3.6×1.2 mm) are a close match for Algerian specimens, but the other two shells are larger (4.2×1.3 and 4.3×1.4 mm) although similar in other respects. It is noteworthy that of the two fresh (translucent) shells, one is colourless and the other is light brown. Gittenberger & Boeters (*op. cit.*, p. 127) noted that Algerian shells appeared to be colourless although 'the few shells known might have faded'.

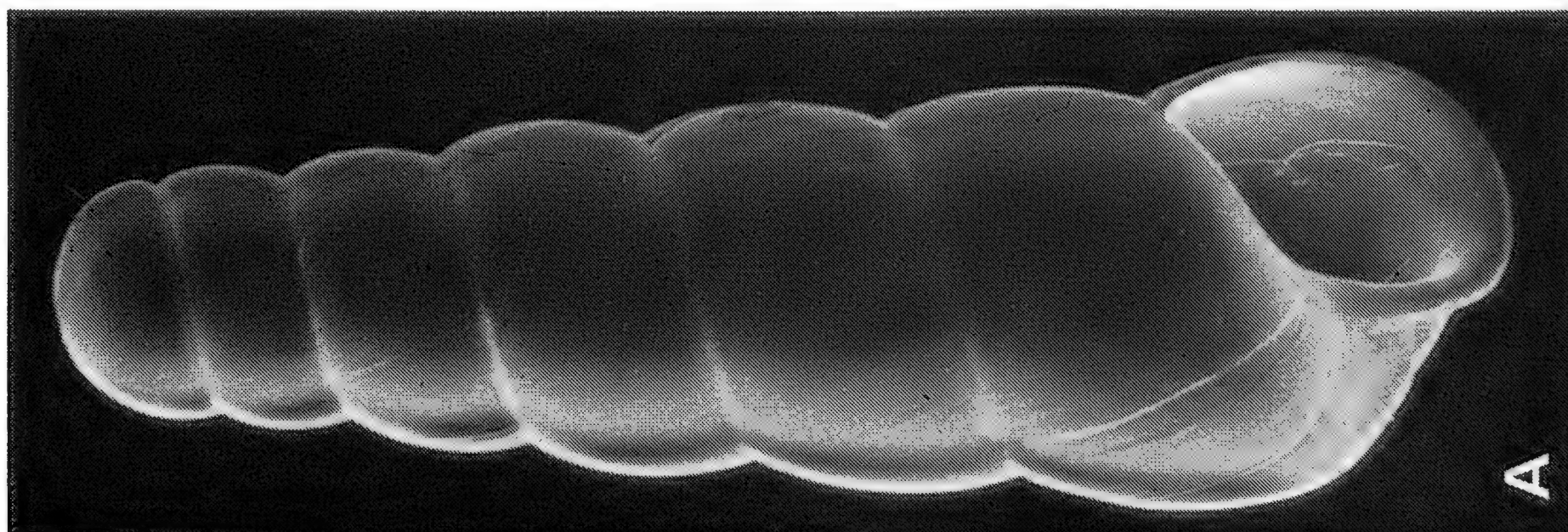
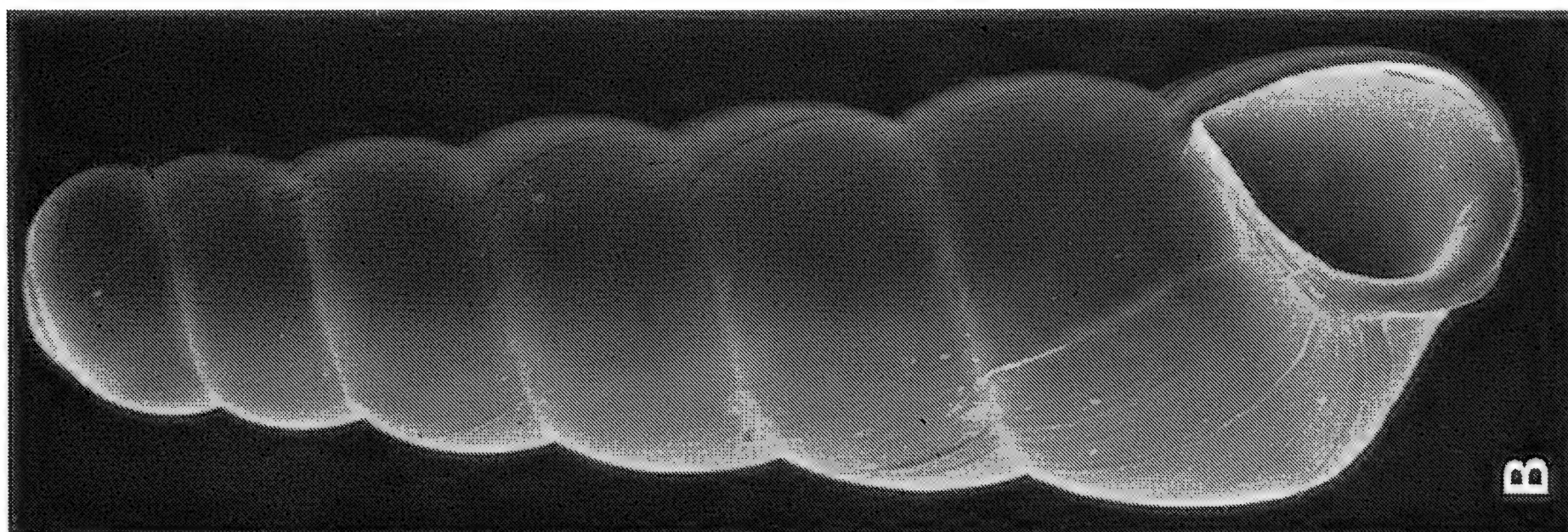
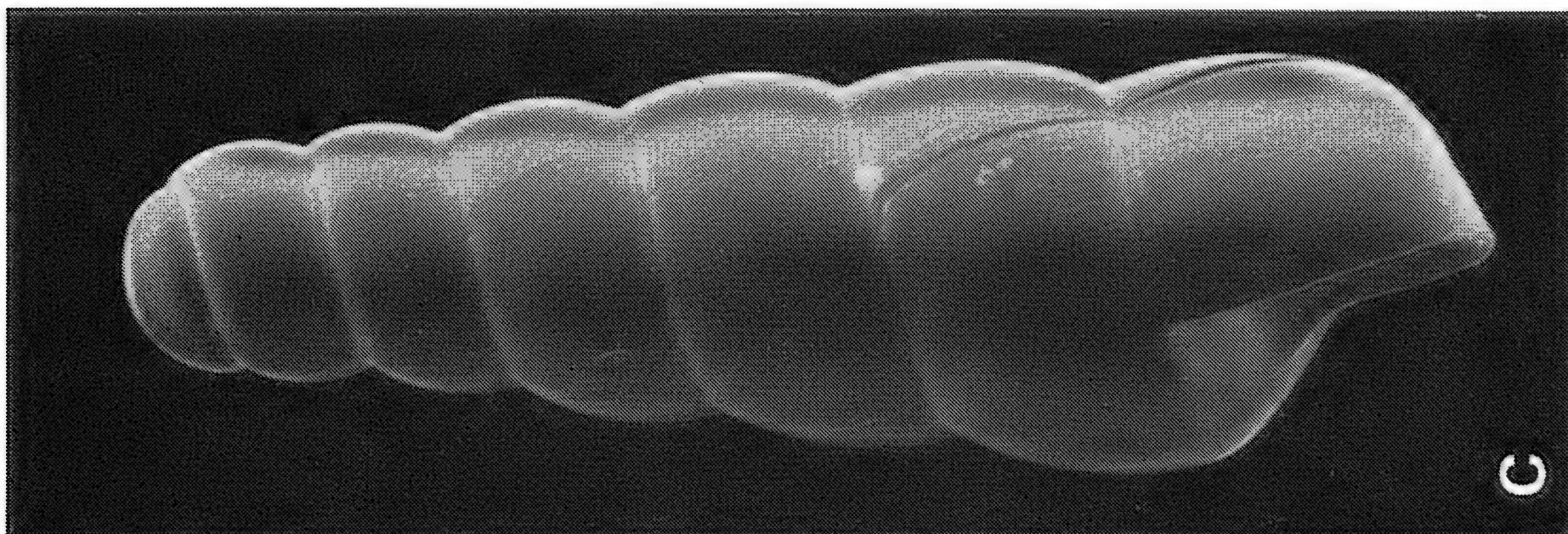


PLATE 8

Shells of *Acicula lusitanica*; A Holotype (height of shell 3.0 mm); B, C Paratypes. Scale marked at intervals of 0.2 mm.

ACKNOWLEDGEMENTS

Thanks are due to M. Holyoak for assistance with fieldwork and to Dr. R. J. Aldridge, Mr. M. P. Smith and Mr. A. Swift of the Department of Geology, University of Nottingham for use of SEM facilities.

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## COMMUNICATIONS

### NON-MARINE GASTROPODA FROM FRANCE, SPAIN AND ITALY

Distributional records of Mollusca collected recently appear to represent extensions of known ranges of several species. For each site the UTM 10 km grid reference is listed in parentheses:

*Cochlostoma obscurum* (Draparnaud) By D960 road 3 km SW of Joinville, Haut-Marne, France (FP 56); mossy limestone wall by road; September 1983. This locality is well north of the range limit shown in eastern France by Kerney, Cameron & Jungbluth (*Die Landschnecken Nord-und Mitteleuropas*, Parey (1983) p. 323).

*Pomatias elegans* (Müller) 4 km SW of Muros, Prov. Pontevedra, Spain (MH 93); on granitic rocks at top of shelving beach beneath patches of herbs; August 1983. Although there are other records of this species in northern and eastern Spain and in Portugal (Kerney, *Arch. Moll.* **106** (1975) p. 246) it has apparently not been reported previously from this north-western part of Spain, which is a region with mainly acidic rocks.

*Pleuracme bayoni* (Pollonera) 1 km N of Riana, Prov. Parma, Italy (NQ 82); one shell from scree of sandstone blocks shaded by saplings and bushes; August 1983. Bishop (*Arch. Moll.* **107** (1976) p. 115) reviewed the status of this rare species which has previously been reported from only two localities in the northern Apennines and two in the Alps (Prov. Novara).

*Acicula cryptomena* (De Folin & Bérillon) By N1 road 2 km W. of Irun, Prov. Vascongadas, Spain (WN 99); roadside bank with masonry, partly shaded by *Hedera*, *Rubus* and trees of *Ulmus* and *Fraxinus*; August 1983. By N625 road c. 3 km S. of Orduña, Prov. Alava, Spain (VN 95); *Fagus* wood on steep limestone hillside; August 1984. These are apparently the first records from Spain of a species hitherto known only from Pyrénées-Atlantiques, France; *Acicula fusca* (Montagu) was found living at both of these sites.

*Acicula callostoma* (Clessin) Floodline debris on bank of River Manol by the C260 road 1½ km W. of Vilafant, Prov. Gerona, Spain (DG 97); August 1983. This species was hitherto known only from the type locality at La Preste, Pyrénées-Orientales, France and from Santa Magdalena de Olot, Prov. Gerona, Spain (Haas, *Trabajos del Museo de Ciencias Naturales de Barcelona* **13** (1929) p. 403).

*Acicula dupuyi* (Paladilhe) A single adult shell from same site as preceding species is apparently the second record from Spain (cf. Bech & Fernandez, *Iberus* **4** (1984) p. 92). The species is widespread in the French Pyrenees (Kerney, Cameron & Jungbluth, *op. cit.*, p. 325).

*Moitessieria rolandiana* Bourguignat Three shells from floodline debris at same site as the two preceding species. Apparently the only other Spanish record is from 'font de la Cirera', Hostalets de Bas, Prov. Gerona (Haas, *op. cit.*, p. 419).

*Cryptazeca monodonta* (De Folin & Bérillon) Known only from a few old records near Bayonne and SE. of Cambo-les-Bains, Pyrénées-Atlantiques, France (Gittenberger, *Zool. Meded., Leiden* **57** (1983) p. 315). Two records from same region made in August 1980 in company with B. Coles and R. C. Preece are from different sites and the first finds this century: Grottes de Sare, c. 15 km SE. of St. Jean-de-Luz (XN 19), sieved from moss and leaf-litter on wooded, rocky, limestone slope; 1 km SW. of Ustaritz (XP 20), sieved from mossy leaf-litter by stream in deciduous wood; more were collected at the Grottes de Sare in August 1983 and August 1984.

*Cryptazeca subcylindrica* De Folin & Bérillon The clear differences between shells of this form and the sympatric *C. monodonta* are described by Gittenberger (*op. cit.*). A few shells found amongst those of *C. monodonta* collected in August 1980, August 1983 and August 1984 at Grottes de Sare bring the total of known sites to four and represent the first records of the species this century.

[*Columella columella* (v. Martens) Tentatively recorded from 3 km below Port de Gavarnie, Hautes-Pyrénées, France (YN 43) by Coles, Holyoak & Preece (*J. Conch., Lond.* **31** (1983) p. 259), but many additional specimens collected from the same place in August 1983 show the characters of *C. edentula* (Draparnaud); thus *C. columella* should be deleted from the list of Pyrenean molluscs.]

*Columella edentula* (Draparnaud) 4 km NW. of Abbadia S. Salvatòre, Prov. Siena, Italy (QN 51) at 1150 m elevation, and nearby on summit of M. Amiata at 1730 m elevation; creeping on tree trunks in woodland during rain; September 1983. These appear to be the first records of this species from the Apennines (cf. Alzona, *Malacofauna Italica* (1971) p. 66; Giusti & Mazzini, *Lav. Soc. Ital. Biogeog.* N.S. (1970) p. 201) although it is locally common in the Italian Alps (e.g. Bishop, *Atti. Soc. ital. Sci. nat. Mus. civ. Stor. nat. Milano* **117** (1976) p. 272).

*Pagodulina austeniana* (Nevill) By D25 road 2 km. E. of Gorníés, Hérault, France (EJ 56); mossy limestone rocks shaded by trees. The shells have three palatal folds and resemble specimens from N. Italy (cf. Gittenberger, *Zool. Verhand., Leiden* **163** (1978) p. 37). *P. austeniana* was originally described from Pleistocene fossils from Menton (Nevill, *Proc. Zool. Soc. Lond.* (1880) p. 130, pl. XIII). Forcart (*Arch. Moll.* **79** (1950) p. 167) regarded it as a

subspecies of *P. subdola* (Gredler), but Gittenberger (*op. cit.*, 1978) shows these are distinct species that coexist in the Italian Alps. Records of *austeniana* from France (Depts. Var, Alpes-Maritimes, Isère and Moselle) were cited by Forcart (*op. cit.*) but these have been overlooked or treated (in some cases perhaps erroneously) as *P. pagodulina* (Des Moulins) in recent publications.

*Granopupa granum* (Draparnaud) By N6 road at Nailly St. More, Yonne, France (EN 57); limestone crag and slopes; August 1983. This locality is well north of the range limit in eastern France shown by Kerney, Cameron & Jungbluth (*op. cit.*, p. 331).

*Pupilla triplicata* (Studer) Unshaded limestone crag by D64 road 5 km S. of Coly, Dordogne, France (CK 69); August 1983. This is further north than records from western France shown by Kerney, Cameron & Jungbluth (*op. cit.*, p. 334), but Preece & Willing (*Conch. Newsl.*, Lond. No. 59 (1976) p. 544) quote a record from near Les Eyzies in Dept. Dordogne.

*Helicodiscus singleyanus* (Pilsbry) Floodline debris on bank of River Manol by C260 road 1½ km W. of Vilafant, Prov. Gerona, Spain (DG 97). The only other record from Spain, is apparently of five shells in the Rijksmuseum, Leiden collected by Altimira from 'detritus del estanque del Mas Turia, Castello de Ampurias, Prov. Gerona' (Altimira, *P. Inst. Biol. Apl.* **46** (1969); E. Gittenberger, *in litt.*). The species has also been recorded from southern France in Hérault (Van Regteren Altena, *Basteria* **25** (1961) p. 41) and Pyrénées-Atlantiques (Coles, Holyoak & Preece, *op. cit.*).

*Vitrea* cf. *diaphana* (Studer) 4 km up road to Col du Couret from Bagnères-de-Bigorre, Hte.-Pyrénées, France (BH 76); a single shell collected while in company with B. Coles and R. C. Preece in August 1980, from mossy ledges of limestone crag shaded by *Fagus*. The shell is 4.1 mm in maximum diameter and lacks any trace of an umbilicus. Riedel (*Fragmenta Faunistica*, Warszawa **15** (1970) p. 381) has shown that in the Pyrénées *V. narbonensis* (Clessin) is the common *Vitrea* with a tiny umbilicus. Older records did not distinguish minutely umbilicate *Vitrea* from those lacking an umbilicus so the older Pyrenean records of *V. diaphana* have been discounted by recent authors (e.g. Kerney, Cameron & Jungbluth, *op. cit.* p. 340).

*Bofilliella subarcuata* (Bofill) Two immature shells from floodline debris on bank of River Manol by the C260 road 1½ km W. of Vilafant, Prov. Gerona, Spain (DG 97); August 1983. This Catalan rarity has apparently only been found about fifteen times, almost always as dead shells (Loosjes & Aleu, *Basteria* **34** (1970) p. 55; Gittenberger, Menkhorst & Raven, *Basteria* **44** (1980) p. 14, Bech & Fernandez, *op. cit.*). Several records from near springs and cave entrances suggest it lives underground, an impression possibly reinforced by the colourless shell and its apparent rarity. Indeed, Nordsieck (*Arch. Moll.* **109** (1978) p. 254) listed the species as 'troglobiont', although Altimira (*Miscelanea. Zool.* **3** (1971) p. 8) has reported it 'en pleno bosque' and Bech & Fernandez found it living on a humid stream bank. Adult shells are decollated (Kerney, Cameron & Jungbluth, *op. cit.*, p. 297) and the immature shell has not been described in the literature. The two specimens measure 2.8 and 6.4 mm in length and are more slender than apices of *Clausilia bidentata* (Ström). The apical 2½ whorls are smooth, glossy and cylindrical; later whorls increase regularly in width and are marked by increasingly strong growth lines. The suture is somewhat more oblique than in *C. bidentata*.

*Cochlodina comensis* (L. Pfeiffer) Known in France only from one find near Digne, Alpes-de-Hte.-Provence (Jaekel, *Arch. Moll.* **92** (1963) p. 79), far to the west of its main range in Italy. In August 1983 a second site was found in Alpes-de-Hte.-Provence by D900 road just S. of la Jarvie (KP 89), beneath *Alnus* and *Salix* on a river bank at 830 m elevation.

*Cochlodina orthostoma* (Menke) By D437 road 2 km SW. of St.-Hippolyte, Doubs, France (LT 34); in deciduous woodland on rocky limestone hillside; September 1983. This is apparently the westernmost record of this species, which is an addition to the French fauna. It is known from the Swiss Jura not far to the east (Mermod, *Cat. Invert. Suisse*, 18, *Gastéropodes Suisse* (1930) p. 386).

*Macrogastra lineolata* (Held) Rocky limestone slope shaded by trees near N116 road about 4 km SW. of Villefranche-de-Conflent, Pyrénées-Orientales, France (DH 41); two living animals collected August 1983; no more were found despite prolonged searching. The two adult shells are small, but otherwise similar to specimens from the French Alps. This species has not previously been recorded from the Pyrenees. Germain (*Faune de France* **21** (1930) p. 363) and Kerney, Cameron & Jungbluth (*op. cit.*, p. 350) do not report its occurrence in southern France west of the Alps and their foothills but a shell in the collection of Mr. Adrian Norris of Leeds was collected by him at the foot of Mt. Ventoux, Vaucluse (FJ 89) in June 1982.

*Macrogastra ventricosa* (Draparnaud) Coles, Holyoak & Preece (*op. cit.*) gave the first record from the French Pyrenees although Haas (*op. cit.*, p. 337) lists an old record from Olot, Prov. Gerona, Spain. In August 1983 we found two other sites in Pyrénées-orientales: 1½ km W. of la Preste on rocky slopes beneath deciduous trees (DG 49); by D115 road 5 km NE. of le Tech on rocky slopes of stream gorge shaded by deciduous trees (DG 59).

*Helicella orzai* Gittenberger & Manga Limestone crag by cave 2 km N. of N1 road by Ibarguren, Prov. Alava, Spain (WN 45); fresh shells; August 1983. Other records of this recently described species (Gittenberger & Manga, *Basteria* **45** (1981) p. 121) are all from the Sierra de Aralar in Prov. Navarra not far northeast of our locality. *Helicella* shells from limestone crags at the Venta de Judas, 4 km NW. of Liedena, Prov. Navarra (XN 32) are generally similar except for the much more weakly developed keel; anatomical study of this form is needed.

## COMMUNICATIONS

*Helicella (Xeropicta) derbentina* (Krynicky) Numerous shells of a puzzling helicellid were collected from rough grassland and edges of salt-marshes 2–3 km N. of Marignane, near Marseilles (FJ 17) in November 1977. They bore a superficial resemblance to shells of *Cernuella neglecta* (Draparnaud), but many were unmarked white and fresher shells had spiral microsculpture on the periostracum. In August 1983 the same form was found living in grassland at a campsite by R. Durance  $\frac{1}{2}$  km NW. of N538 road near Cavaillon (FJ 65).

Anatomical study of the 1983 specimens showed a combination of characters different to those of any well known French Helicidae and distinctive of *Helicella* subgenus *Xeropicta* (cf. Likharev & Rammelmeier, *Terr. Moll. Fauna USSR* (1962) p. 484). Noteworthy features of the distal genitalia were: two pairs of small dart sacs, the proximal pair longer and thinner, without darts; four mucous glands, each of them with one or two branches; penis short and thick with a tapering penial appendage of similar size to penis and originating near its distal end; epiphallus about six times as long as penis, with short slender flagellum; short retractor muscle attached to distal end of epiphallus.

Species of *Helicella (Xeropicta)* range eastwards from the Balkans and Egypt to the Middle East and Central Asia in the USSR. In the Balkans, *H. (X.) krynickii* (Krynicky) appears to have been more widely recorded in the literature than *H. (X.) derbentina* (Jaekel, Klemm & Meise, *Abhandl. Bericht. Staatl. Mus. Naturk. Dresden* **23** (1957) pp. 163, 187), with records of the latter only from Bulgaria (cf. Damjanov & Likharev, *Fauna Bulg.* **4**, *Gastr. Terr.* (1975) p. 357). However, shells similar to *derbentina* were collected by us at two localities in northern Greece in April 1981: 2 km S. of Petroussa (c. 15 km W. of Drama) (KF 56), and 2½ km NE. of Damasouli by the E90 road (c. 40 km NW. of Larissa) (EJ 99). These Greek shells resemble those from France in having a less excentric umbilicus than that of *H. (X.) krynickii*, allowing the entire penultimate turn to be seen in the umbilicus (cf. Likharev & Rammelmeier, *op. cit.*, p. 483), but conchological characters are insufficiently distinctive for positive identification.

There are few previous records of *H. (X.) derbentina* in western Europe. Van Regteren Altena (*Basteria* **24** (1960) pp. 21–26) reported *Xeropicta* in France, but this paper has been overlooked by most recent authors. In addition, Dr. E. Gittenberger (*in litt.*) has pointed out that the record of '*Helicella arenosa* Ziegler' given by Bonavita (*Publ. Univ. Aix-Marseille, Ann. Fac. Sci. Marseille* **38** (1965) pp. 85–107) should also be referred to *Xeropicta*.

*Cernuella neglecta* (Draparnaud) By D749 road on S. edge of Bourgueil, Indre et Loire, France (BN 78); on unshaded tall herbs near wall of bridge; August 1983. Identification checked by dissection. Not recorded from this part of France by Clerx & Gittenberger (*Zool. Meded., Leiden* **52** (1977) p. 27) nor Kerney, Cameron & Jungbluth (*op. cit.*, p. 355) although there are records from the Dordogne and from eastern and southern France.

*Trochoidea geyeri* (Soós) By D710 road 3 km S. of Mazeyrolles, Dordogne, France (CK 44); empty shells collected from old limestone quarry; August 1983. Also, by D129 road 1 km N. of Anduze, Gard, France (EJ 77); empty shells from ledges of limestone crags; August 1983. Apparently, the only other record from southern France is from Ariège (Coles, Holyoak & Preece, *op. cit.*).

*Ashfordia granulata* (Alder) By N634 road 6 km east of Llanes, Prov. Oviedo, Spain (UP 60); limestone crag with herbs on ledges; August 1983. There are few previous records from Spain: Bishop (*Arch. Moll.* **107** (1976) p. 111) reported old museum specimens labelled 'Gijón', i.e. Prov. Asturias and Manga (*Los Helicidae (Gastropoda, Pulmonata) de la Provincia de León* (1983) León) gives records from Prov. León.

We are grateful to Dr. E. Gittenberger for helpful comments on a draft of this note.

D. T. HOLYOAK AND MARY B. SEDDON

Department of Geography, University of Nottingham, Nottingham NG7 2RD

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## ARION INTERMEDIUS NORMAND 1852 IN SOUTHERN ITALY

Whilst studying the smaller Arionidae in the collections of the Naturhistorisches Museum Basel, I found a sample from S. Italy labelled *Arion hortensis* de Férussac 1819 (NMB 4577-ak). It contains three specimens, two, of which are correctly identified although they are juveniles. The third specimen should, however, undoubtedly be referred to *A. intermedius*. The specimen was recognised by its yellowish-gray colour and by the tubercles which stand up in little conical eminences. The latter feature is usually not apparent in alcohol material, but in this sample it is nevertheless quite visible. The sample was taken by Dr. L. Forcart (Basel) on 15 May 1960 at Aspromonte near Cambaria (prov. Reggio di Calabria) in the southern tip of the Italian peninsula. The slugs were collected at an altitude of about 1400 m. The sample was used in a study by Dr. Forcart of the land molluscs of southern Italy (*Verhandl. Naturf. Ges. Basel* **76** (1965) pp. 59–184), so his list should also include *A. intermedius*. In Italy this species was recorded by Alzona from the Alpi Carniche, Alto Adige and Toscana (*Atti. Soc. ital. Sci. nat.* **111** (1971) pp. 1–433). Dr. Forcart's record therefore extends the distribution of the species far to the south. Kerney *et al.* further reported *A. intermedius* from S. Iceland, S.W. Norway, S. Sweden, Denmark, W. Poland, Czechoslovakia, W. and



E. Germany, The Netherlands, Belgium, W. France, Great Britain, Ireland and Austria (*Die Landschnecken Nord- und Mitteleuropas* (1983), p. 146 and p. 338 map 142). In addition Quick reported the species from Portugal, Spain, N. Italy, Russia and the Azores (*Bull. Brit. Mus. (Nat. Hist.)* **6** (1960), p. 127).

I would like to thank Dr. L. Forcart and the staff of the Basel Museum for their permission to study this material.

THIERRY BACKELJAU

Laboratorium voor Algemene Dierkunde, Rijksuniversitair Centrum Antwerpen, Groenenborgerlaan 171, B-2020 Antwerpen, Belgium.

(Received, 15 November 1984)

## IDENTITY OF *CONUS*—A CORRECTION

A few days ago I received a letter from Mr. Alison Trew of the National Museum of Wales, pointing out to me that the registration number of the holotype of *Conus baccatus* Sowerby is 1955.158.29, and not 34.01.29 as I had cited in my recent article in the Journal of Conchology **31** (1984) pp. 353–357, entitled 'On the identity of *Conus anaglypticus*, *Conus baccatus*, *Conus selenae* and *Conus yemanjae*'. Whereas in the case of citations of other registration numbers I verified the numbers with the museums concerned, in the case of *C. baccatus* I had copied the number from Coomans, Moolenbeek & Wils in their *Alphabetical revision of the (sub) species in recent Conidae 5. baccatus to byssinus*, etc. in *Basteria* **46** (1982) pp. 3–67.

D. L. N. VINK

Prinsenweg 73, 2242 EC Wassenaar, Holland

(Received, 19 November 1984)

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# INFRALITTORAL MACROBENTHOS OF THE PATRAS GULF AND IONIAN SEA: OPISTHOBRANCH MOLLUSCS

T. E. THOMPSON<sup>1</sup>, G. M. JARMAN<sup>1</sup> AND A. ZENETOS<sup>2</sup>

(Accepted for publication, 22 February 1985)

**Abstract:** Surveys carried out in the summers of 1981 and 1982 revealed 19 macrobenthic species, the most varied assemblage of infaunal and epifaunal opisthobranchs yet reported. The study-area consisted of 4 sectors: the Patras Gulf, Zakynthos and Kefallonia islands, and the Ionian Sea coast of the northern Peloponnese. The Patras Gulf sector contained the finest sediments; sand was the dominant type in the other 3 sectors. The infaunal carnivore *Philine aperta* was the most prevalent opisthobranch in the study-area as a whole, followed closely by the herbivorous *Haminea navicula* and the carnivorous *Weinkauffia diaphana*. Some species, like *Cylindrobulla fragilis*, were purely herbivorous. Others were micro-carnivores, feeding on infaunal foraminiferans, annelids and bivalved molluscs (e.g. *Cylichna cylindracea*, *Rhizorus acuminatus*, *Acteon tornatilis*, *Aglaja tricolorata* and *Retusa truncatula*).

Biogeographically there are 4 categories represented in the samples: (a) an indigenous Mediterranean component (27.8%), (b) a Mauretanian component (16.7%), (c) a Lusitanian component (27.8%), and (d) a group of eastern Atlantic cosmopolitan species (27.8%), of which 2 species (11.1%) penetrate as far as the Black Sea. There is no evidence that the epifaunal species are more widespread than the infaunal species. No Lessepsian immigrants could be identified.

A significant positive correlation between opisthobranch species-diversity and mean grain-size was found only in the Kefallonia samples. A comparison between the Jaccard and Matching coefficient methods of expressing ecological affinity between opisthobranch species showed the superiority of the former method for our data. This was because the Matching coefficient method gave undue weight to the number of conjoint absences in the samples. Foremost among the examples of significant similarities was the association between *Bulla striata* and *Cylindrobulla fragilis*, between *Weinkauffia diaphana* and *Atys jeffreysi* and between *Rhizorus acuminatus* and *Retusa* agg. In the first pair there is probably a trophic cause for the association, but in the other examples it is probable that the protagonists are correlated not with each other directly but with some abiotic factor.

## INTRODUCTION

Published knowledge concerning the opisthobranch molluscs of the eastern Mediterranean has been sparse, and so far has consisted only of faunistic recording (Forbes 1844, critically revised by Nordsieck 1977, Swennen 1961: the Netherlands expedition to Turkey (1959), Pérès & Picard 1958: dredging from the *Calypso*, O'Donoghue & White 1940: Palestine, Eales 1970 and Barash & Danin 1972: Lessepsian immigration). Furthermore, there have been reports published on the opisthobranch molluscs of Cyprus by Demetropoulos (1969, 1971) and Demetropoulos & Hadjichristophorou (1976). In such attempts to map the opisthobranchs of Greek waters, it is disappointing to learn that Forbes's pioneering efforts were largely wasted. His collections were dispersed, given or loaned to friends and often lost. Unaccompanied by voucher material, his descriptions were often so general that they are useless. His dredging stations in the Aegean (of which there were more than 100, at 2-65 m depth) were investigated over more than a year in H.M.S. *Beacon*. His 15 species of nudibranchs and 6 of pleurobranchs are nearly all unrecognizable, and the status of the 18 species of bullomorphs is even worse. Nordsieck (1977) made a painstaking effort to match

<sup>1</sup> Zoology Department, University of Bristol, U.K.

<sup>2</sup> Zoological Laboratory, University of Athens, Panepistimiopolis 621, Greece.



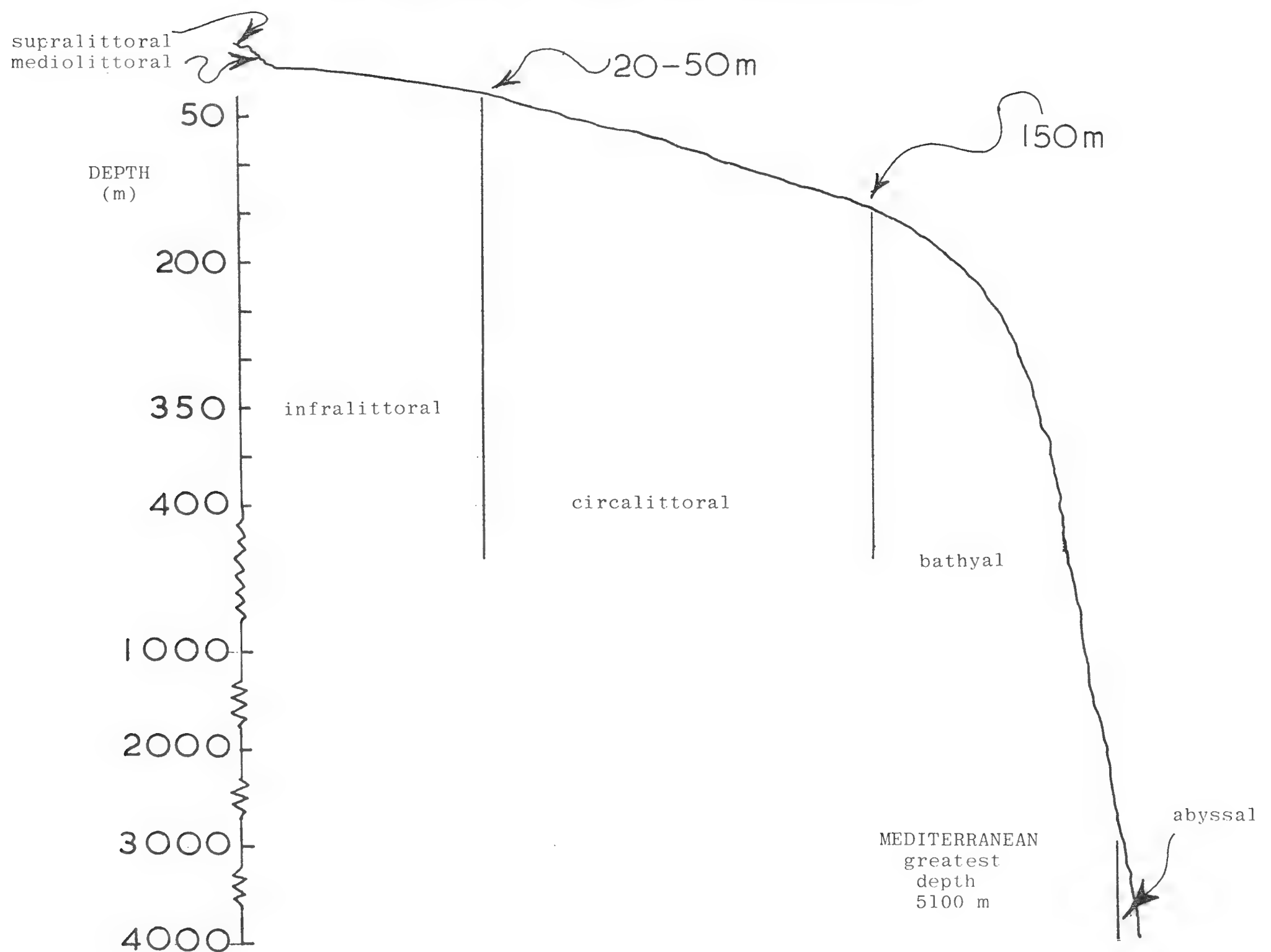


Fig. 1. Diagram showing nomenclature employed, after Pérès, 1967.

Forbes's Latin diagnoses with modern Mediterranean taxa. So far as the opisthobranchs are concerned (excluding the pyramidellids), Nordsieck was able to match only 6 of Forbes' species with present-day forms. With all the types apparently lost, this is probably the best that can be done.

The Gulf of Patras was chosen for our initial survey work because it had been the area studied in circalittoral surveys carried out by the Greek Institute of Oceanographic and Fisheries Research (Bogdanos & Nicolaidou 1984). The ultimate aim will be to provide materials for a synthesis of the biota encountered in the two surveys. In our second survey year (1982), the boundaries were expanded to take in the Ionian Sea coast of the Peloponnese and the islands of Zakynthos and Kefallonia. This expansion has enabled comparisons to be made of different environmental conditions within the same biogeographic area. Our aim was to examine the opisthobranch molluscs of the area, to quantify endemism, to seek evidence of clustering or community-formation and to relate animal distribution to certain abiotic parameters.

The west coast of Greece borders some of the greatest depths in the Mediterranean Sea. It is a meeting place for many different components of the fauna of this apparently circumscribed basin, with Lusitanian and Mauretanian elements as well as both Adriatic and Lessepsian biota (Pérès 1967, Por 1971). It was once the scene of luxuriant coral reefs (in the Cretaceous period) but these no longer survive, even though the summer shallow sea-water temperatures in the eastern Mediterranean are subtropical (25–27°C.), because the winter temperatures fall to 10°C. or lower.

The Patras Gulf is a busy commercial waterway, leading to the Gulf of Corinth; the bottom is generally less than 80 m deep, shelving to 650 m in the Ionian Sea on the westward sides of the islands, and reaching 2000 m off the western coasts of the Peloponnese. It lies on the biogeographical border separating the central and northern parts of the eastern Mediterranean basin (Pérès 1967), near the straits of Otranto and the rich 'Boka Kotorska' fishing grounds of the southern Adriatic Sea (Gamulin-Brida 1967).

Although tidal effects are significant in several parts of the Mediterranean Sea, they usually take the form of tidal streams leading to surfless turbulence rather than substantial oscillations in elevation. Tidal currents in the Strait of Messina can reach 2 m/sec, similar to the flow under the Khalkis Bridge connecting the island of Evia with the Greek mainland of Attica. In rare situations, significant vertical tide amplitudes have been reported; the best known example is in the Tunisian Gulf of Gabès (2.2 m at spring tides, according to Pérès 1967). There are only small tidal influences in the southern Adriatic Sea in and around the Gulf of Patras (the vertical amplitude rarely exceeds 0.6 m). Such changes in sea-level are insignificant compared with wind-generated perturbations. It seems best, therefore, to employ the terminology of Pérès (1967), proposed as the result of his broadly based review of studies of the Mediterranean benthos. A simplified diagram represents his recommended usage (Fig. 1). Richards (1983) has recently attempted to adapt the Stephenson (1949) and Lewis (1964) scheme of nomenclature to shores in the Mediterranean. The wisdom of this attempt may be questioned because the Stephenson/Lewis scheme of zonation was derived from studies of hard substrata in areas where lunisolar tides were substantial. Richards (1983) does not mention the well established scheme advocated by Pérès.

The Pérès scheme applies to both hard and soft substrata. Broadly speaking, animals tend to dominate the biota in the circalittoral zone (especially where the bottom is cloaked with sediments), whereas the infralittoral zone tends to be dominated by plants, especially the phanerogams ('sea-grasses') in regions of soft substrata. In the Mediterranean Sea the infralittoral/circalittoral boundary is at about 20 m depth in high latitudes and turbid waters, and at about 50 m in low latitudes and clearer waters. All the macrobenthos obtained in the present surveys of the Patras Gulf and its vicinity came from the infralittoral zone, to 15 m depth, in soft substrata.

## METHODS

The only published data relevant to the present study show that the water temperatures in the Harbour at Patras ranged from 13 to 17°C in January and from 22 to 26°C in August (Souri-Kouroubali 1976). The surface water salinity measured approximately 38‰ throughout the year (Piper & Panagos 1979).

The Patras Gulf samples were taken in July and August, 1981; the other sites were sampled in July and August, 1982. Depth was determined by cable or sonar. At each site dredge-samples were taken at two stations, 5 and 15 m deep, using a Forster's anchor dredge (Holme 1961), which is a semi-quantitative sampler having a biting depth of 15–25 cm (Holme 1971, Gage 1972). The total number of sites sampled was 173; 2–4 separate dredge-hauls were obtained from each station. Subsamples were preserved in dilute (4%) formalin with dissolved rose-bengal for sorting in the Athens laboratory. Other aliquots were kept for grain-size analysis, following the method of Bowles (1978).

Our salinity measurements (made using a refractometer) normally ranged from 38–41‰. In close proximity to the inlets of Evinos and Alfios the salinity dropped locally to 21.5 and 18‰, respectively.

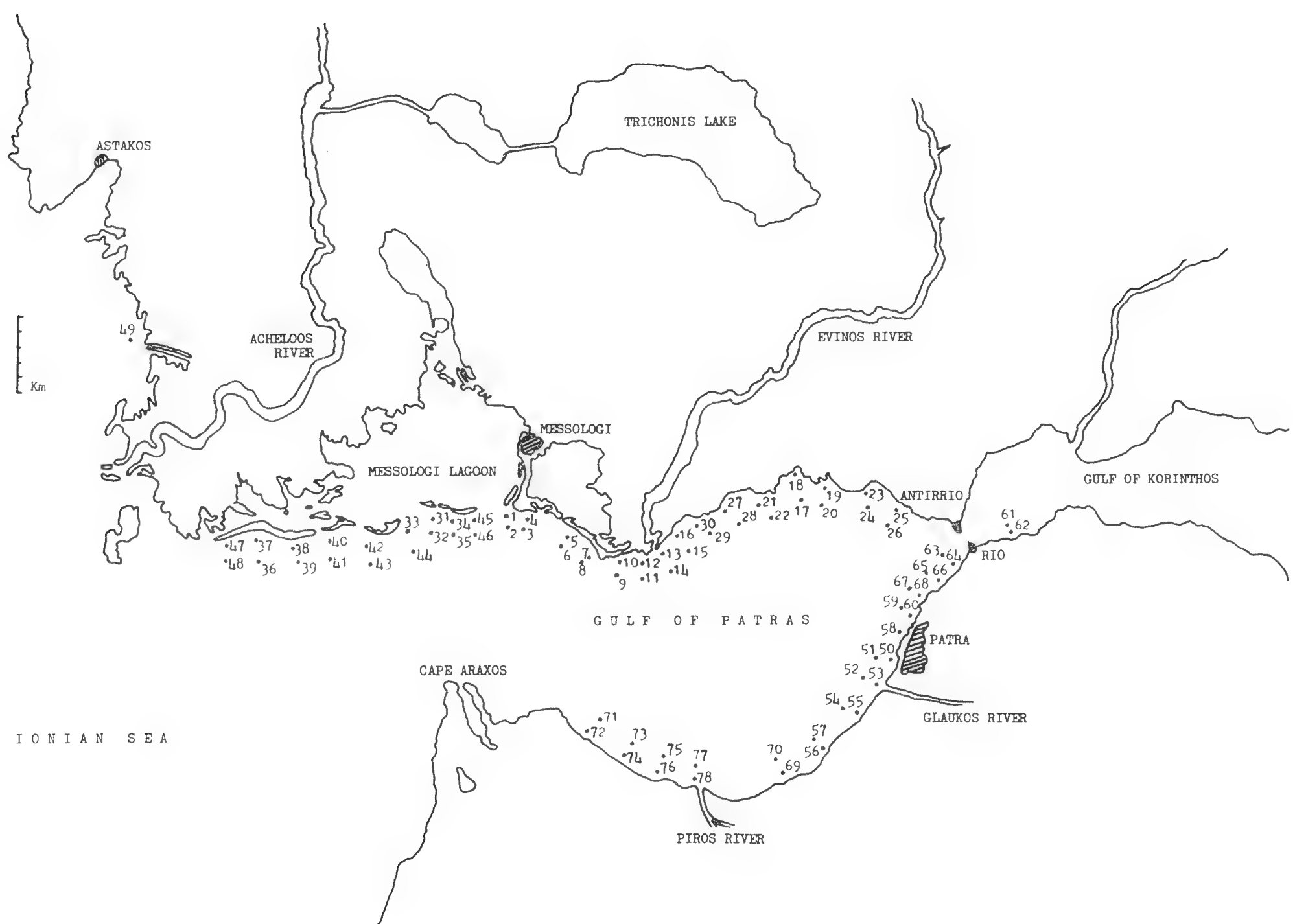


Fig. 2. Map showing the location of sampling stations in the Gulf of Patras.

Surface water temperatures in the shallow waters of the Patras Gulf and its immediate vicinity tended to fluctuate diurnally. In the Gulf proper the diurnal range was 19–27°C; in the Ionian Sea sector it was 24–27°C; around Zakynthos it was 25–28°C and around Kefallonia it was 26–27.5°C (July–August measurements).

## RESULTS

### SEDIMENTOLOGY

The distribution of sediment types in the four sectors Gulf of Patras (PA) Peloponnese coast bordering the Ionian Sea (IO), Zakynthos (ZA) and Kefallonia (KE) is shown in Table 1.

It is clear from the table that the sheltered waters of the Gulf of Patras overlie the sediments containing the lowest proportion of sand, while in the other three sectors sand was the dominant type. This appears to correlate well with the known greater influence of sea water currents in the Ionian Sea with the consequent creation of high energy environments.

### PREVALENCE OF OPISTHOBRANCHIA

Table 2 summarises the prevalence data derived from the dredged samples. The species are



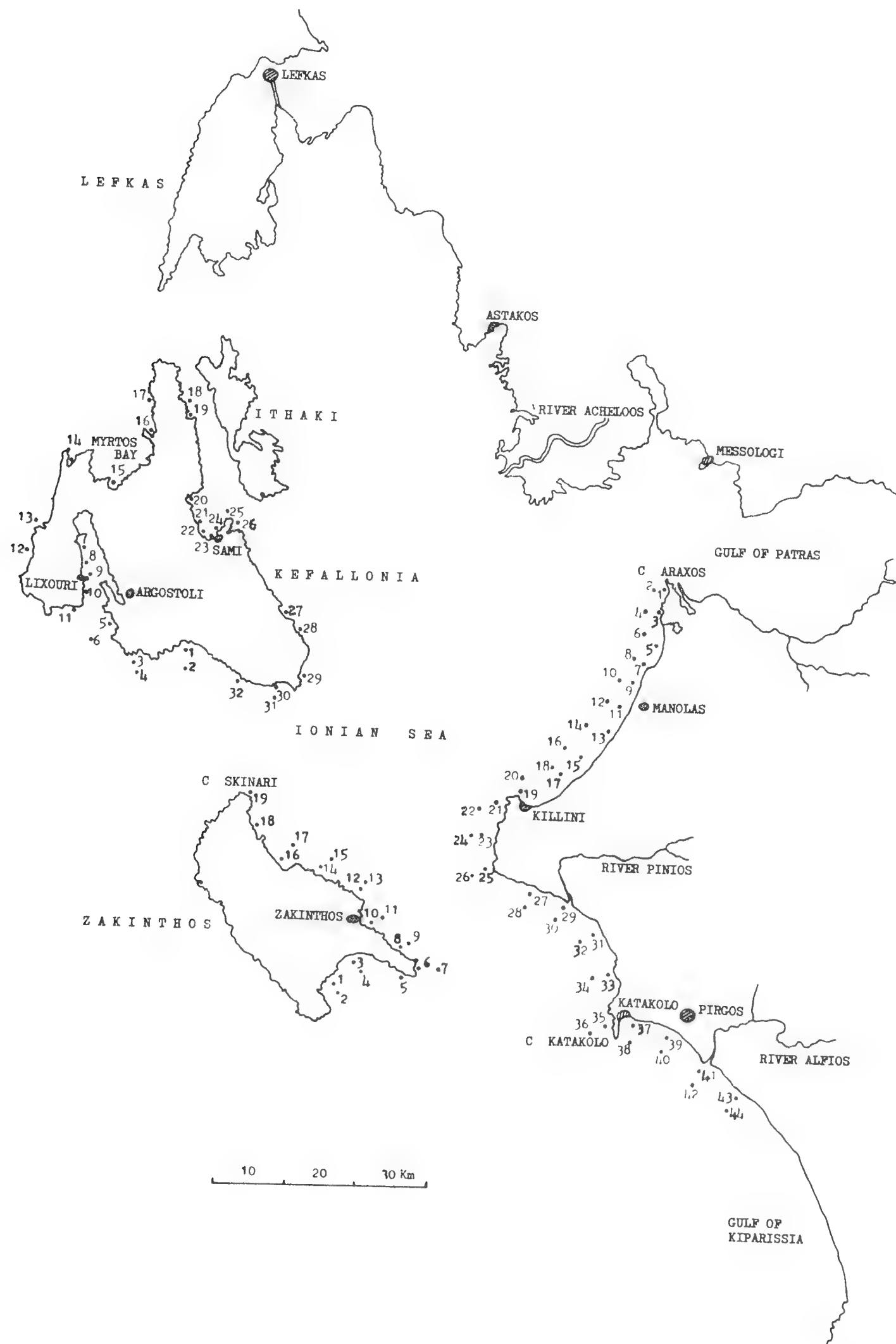


Fig. 3. Map showing the location of sampling stations around the islands of Kefallonia and Zakynthos, and off the Ionian Sea coast of the Peloponnese.

arranged in order of decreasing overall prevalence. The first two columns are derived from pooled data from the whole study area, but the remaining columns present separately data from the four sectors of the study area. These data show that *Philine aperta* was the most prevalent opisthobranch species in the study area as a whole, followed closely by *Haminea navicula* and *Weinkauffia diaphana*. But *P. aperta* was not the most common opisthobranch in all the sectors; in Zakynthos the most common form was *Atys jeffreysi*. Some species were absent altogether from one or more of the sectors, for example, *Petalifera petalifera* was present in the Ionian Sea and Patras Gulf samples, but absent in those from Zakynthos and Kefallonia. This is a herbivorous species, feeding upon algae. The relative prevalence of the opisthobranch species in the four sectors of the study-area is shown in Fig. 4.

TABLE 1

Proportions of sediment types in the different sectors of the study-area

	PA	IO	ZA	KE
% mud	1.72	—	—	—
% sandy mud	13.79	2.56	—	3.7
% sandy silt	20.69	7.69	—	3.7
% silty sand	15.52	17.95	7.14	11.11
% muddy sand	12.07	10.25	—	3.7
% sand	36.20	61.54	78.57	55.55
% coarse sand and gravel	—	—	14.28	22.22

(nomenclature after Folk 1954)

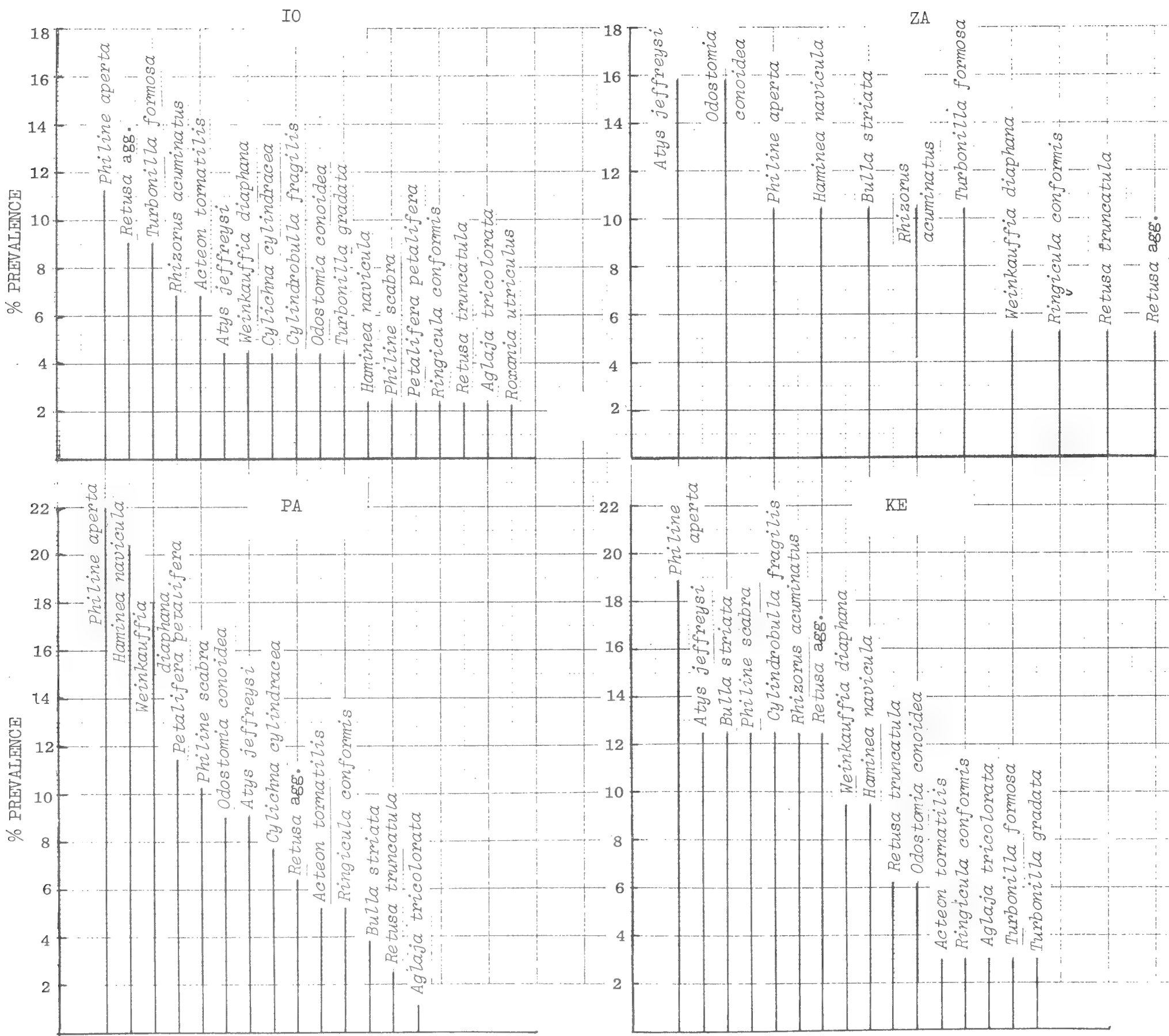


Fig. 4. Prevalence of opisthobranch species in the four sectors of the study area.

TABLE 2

Prevalence of opisthobranch species in the benthos samples

THOMPSON, JARMAN & ZENETOS: OPISTHOBRANCH MOLLUSCS												
	All data (173 stations)		PA (78 stations)		IO (44 stations)		KE (32 stations)		ZA (19 stations)			
	Total number of stations	% prevalence	Number of stations	% occurrence	Number of stations	% occurrence	Number of stations	% occurrence	Number of stations	% occurrence		
<i>Philine aperta</i>	30	17.34	17	21.79	5	11.36	6	18.75	2	10.53		
<i>Haminea navicula</i>	22	12.72	16	20.51	1	2.27	3	9.38	2	10.53		
<i>Weinkauffia diaphana</i>	20	11.56	14	17.95	2	4.55	3	9.38	1	5.26		
<i>Atys jeffreysi</i>	16	9.25	7	8.97	2	4.55	4	12.50	3	15.79		
<i>Odostomia conoidea</i>	14	8.09	7	8.97	2	4.55	2	6.25	3	15.79		
<i>Retusa</i> agg.	14	8.09	5	6.41	4	9.09	4	12.50	1	5.26		
<i>Philine scabra</i>	13	7.51	8	10.26	1	2.27	4	12.50	0	0		
<i>Petalifera petalifera</i>	10	5.78	9	11.54	1	2.27	0	0	0	0		
<i>Bulla striata</i>	9	5.20	3	3.85	0	0	4	12.50	2	10.53		
<i>Rhizorus acuminatus</i>	9	5.20	0	0	3	6.82	4	12.50	2	10.53		
<i>Acteon tornatilis</i>	8	4.62	4	5.13	3	6.82	1	3.13	0	0		
<i>Cylichna cylindracea</i>	8	4.62	6	7.69	2	4.55	0	0	0	0		
<i>Ringicula conformis</i>	7	4.05	4	5.13	1	2.27	1	3.13	1	5.26		
<i>Turbonilla formosa</i>	7	4.05	0	0	4	9.09	1	3.13	2	10.53		
<i>Cylindrobulla fragilis</i>	6	3.47	0	0	2	4.55	4	12.50	0	0		
<i>Retusa truncatula</i>	6	3.47	2	2.56	1	2.27	2	6.25	1	5.26		
<i>Aglaja tricolorata</i>	3	1.73	1	1.28	1	2.27	1	3.13	0	0		
<i>Turbonilla gradata</i>	3	1.73	0	0	2	4.55	1	3.13	0	0		
<i>Roxania utriculus</i>	1	0.58	0	0	1	2.27	0	0	0	0		

The four sectors of the study-area are abbreviated PA (Patras Gulf), IO (Ionian coast of the Peloponnese), KE (Kefallonia) and ZA (Zakinthos). Sampling stations are shown in Figs. 2 & 3.



TABLE 3  
Diet and geographical distribution within the Mediterranean Sea of opisthobranch species identified in the survey samples

Opisthobranch species	Eastern Basin					Diet
	Alboran Sea <sup>1</sup>	Western Basin <sup>2</sup>	Adriatic Sea <sup>3</sup>	Southern and eastern areas <sup>4</sup>	Central and northern areas <sup>5</sup>	
<i>Acteon tornatilis</i>	+	+	+	+	+	thecate
<i>Bulla striata</i>	+	+	+	+	+	Protozoa
<i>Atys jeffreysi</i>	+	+		+	+	omnivore
<i>Weinkauffia diaphana</i>	+	+		+	+	carnivore
<i>Haminea navicula</i>	+	+	+		+	carnivore
<i>Ringicula conformis</i>	+	+	+		+	herbivore
<i>Cylichna cylindracea</i>	+	+	+		+	carnivore
						thecate
<i>Roxania utriculus</i>	+	+	+		+	Protozoa
<i>Rhizorus acuminatus</i>	+	+	+		+	unknown
<i>Retusa truncatula</i>	+	+	+		+	unknown
<i>Retusa</i> agg.						carnivore
<i>Philine aperta</i>	+	+	+	+	+	carnivore
<i>Philine scabra</i>	+	+	+		+	carnivore
<i>Aglaja tricolorata</i>		+	+		+	predator
<i>Odostomia conoidea</i>	+	+		+	+	ectoparasitic
<i>Turbonilla formosa</i>	+				+	ectoparasitic
<i>Turbonilla gradata</i>		+			+	ectoparasitic
<i>Petalifera petalifera</i>	+	+			+	herbivore
<i>Cylindrobulla fragilis</i>	+	+			+	herbivore (roots)

Sources:

<sup>1</sup> Altimira *et al.* 1981, Luque 1983, Ortea 1976, 1977, Ros 1975, 1976, Ros & Altimira 1977, Templado 1982, Templado *et al.*, 1983.  
<sup>2</sup> Fasulo *et al.* 1982, Haefelfinger, 1960. Mangold-Wirz & Wyss 1958, Parenzan 1970, Pruvot-Fol 1954, Sordi 1969, Tchang-Si 1931, Terreni 1981.  
<sup>3</sup> Coen 1937, Vatova 1928, Thompson 1984, Zavodnik 1971.  
<sup>4</sup> O'Donoghue & White 1940, Barash & Danin 1972.  
<sup>5</sup> Demetropoulos 1969, 1971, Demetropoulos & Hadjichristophorou 1976, Forbes 1844, Swennen 1961, Present study.

TABLE 4  
Geographical distribution of opisthobranch species identified in the survey samples

Opisthobranch species	Black Sea	Eastern Mediterranean	Western Mediterranean	Mauretanian (Canaries, Madeira W. Africa)	Lusitanian (Biscay, British Is., Scandinavia)	West Indies	Cape of Good Hope
<i>Petalifera petalifera</i>		+	+				
<i>Atys jeffreysi</i>		+	+				
<i>Aglaja tricolorata</i>		+	+				
<i>Turbonilla gradata</i>		+	+				
<i>Weinkauffia diaphana</i>		+	+				
<i>Cylindrobulla fragilis</i>		+	+	+			+
<i>Philine aperta</i>		+	+	+	+		
<i>Bulla striata</i>		+	+	+		+	
<i>Odostomia conoidea</i>		+	+	+	+		
<i>Cylichna cylindracea</i>		+	+	+	+		
<i>Roxania utriculus</i>		+	+	+	+		
<i>Ringicula conformis</i>		+	+		+		
<i>Rhizorus acuminatus</i>		+	+		+		
<i>Philine scabra</i>		+	+		+		
<i>Acteon tornatilis</i>		+	+	+	+		
<i>Turbonilla formosa</i>		+	+		+		
<i>Retusa truncatula</i>	+	+	+	+	+		
<i>Haminea navicula</i>	+	+	+	+	+		

Sources: Fasulo *et al.* 1982, Marcus & Marcus 1968, Milashewich 1916, Nordsieck 1972, Pruvot-Fol 1954, Thompson 1976, 1977, Personal observations.

The trophic relationships among these opisthobranchs are complex (Table 3). Some, like *Cylindrobulla fragilis* (which probably feeds on *Caulerpa* rootlets), *Haminea navicula* (feeding upon green filamentous algae), and the *Petalifera* referred to above, are purely herbivorous. Others are micro-carnivores, like *Cylichna cylindracea*, *Rhizorus acuminatus*, *Philine aperta* and *P. scabra*, *Acteon tornatilis*, *Aglaja tricolorata* and *Retusa truncatula*, feeding upon infaunal foraminiferans, annelids and bivalved molluscs. Pyramidellomorphs such as *Odostomia* and *Turbonilla* are known to be ectoparasitic forms, feeding suctorially on a variety of invertebrate hosts.

#### BIOGEOGRAPHY

Tables 3 and 4 summarise what is known about the recorded distribution of the opisthobranch species sampled. Table 3 emphasises the geographical subdivision of the Mediterranean Sea advocated by Pérès (1967), whereas Table 4 divides the Mediterranean arbitrarily into eastern and western moieties and considers correlations between the opisthobranch fauna of the study area and that of other parts of the Atlantic Ocean.

Leaving aside the problematic *Retusa* agg., it is clear that the study-area contains species which are widespread in the Mediterranean Sea, in both major subdivisions; none can be considered to be endemic to Greek waters. All the biogeographic affinities are with the Atlantic Ocean. There appear to be four distributional categories (Table 4):

- (a) an indigenous Mediterranean component, 5 species (27.8%).
- (b) a Mauretanian component, 2 species (11.1%).
- (c) a Lusitanian component, 4 species (22.2%).
- (d) eastern Atlantic cosmopolitan component, 7 species (38.9%), of which 2 species (11.1%) penetrate as far as the Black Sea.

There is no evidence that the epifaunal species are any more widespread in distribution than the infaunal species. The greatest distributional range noted was for *Philine aperta*, which occurs abundantly in soft subtidal substrata from Scandinavia to the Cape of Good Hope.

In contrast to other invertebrate groups, even as closely related as the nudibranchs (Thompson & Crampton 1984), there is no evidence in the samples of Lessepsian immigration. The opisthobranch fauna of the study-area is evidently stable and well established.

#### ABIOTIC CORRELATIONS

Correlations were sought between species-diversity and mean grain size of the substratum, considering the four sectors of the study-area separately. Moreover, the Patras Gulf samples were considered in two moieties, one consisting of stations in the north of the Gulf and the other consisting of stations in the south. Table 5 shows Spearman's non-parametric rank-correlation coefficients calculated for each sector.

A significant correlation emerges (marked with \*) only around the island of Kefallonia; it is uncertain why such a correlation is absent in the other sectors. The opisthobranch fauna in all the subdivisions contains a preponderance of infaunal species, which might be expected to be dependent upon such physical characters of the substratum. This is probably an increasingly significant factor in areas of coarser sediment constitution. The range of sediment types is described for each species below.



TABLE 5

Correlations between substratum particle-size and opisthobranch species-diversity

Study area sector	mean grain size/number of species	% mud/number of species
North PA (n=34)	$r_s = -0.288$ $p > 0.05$	$r_s = 0.245$ $p > 0.10$
South PA (n=24)	$r_s = -0.243$ $p > 0.20$	$r_s = 0.192$ $p > 0.20$
IO (n=39)	$r_s = -0.299$ $p > 0.05$	$r_s = 0.195$ $p > 0.20$
ZA (n=13)	$r_s = 0.081$ $p > 0.50$	$r_s = 0.356$ $p > 0.20$
KE (n=29)	$r_s = -0.701^*$ $p < 0.01$	$r_s = 0.58^*$ $p < 0.01$

 $r_s$  = correlation coefficient

n = number of stations

mean grain size and % mud calculated according to the methods of Bowles (1978) and Briggs (1977).

## BIOTIC CORRELATIONS

Ecological affinity between opisthobranch species was evaluated using both the Jaccard and Matching coefficients (Clifford & Stephenson 1975, Goodall 1978). The former was based upon the formula  $a/(a+b+c)$ , whereas the latter employed  $(a+d)/(a+b+c+d)$ , where  $a$  = the number of conjoint presences in the samples,  $b$  = one species present the other absent,  $c$  = the opposite circumstance to  $b$ , and  $d$  = the number of conjoint absences.

In practice, it was found that there were too many conjoint absences for the effective application of the Matching coefficient evaluation of ecological affinity. This was because this method of evaluation gave undue weight to the number of conjoint absences, so that a high Matching coefficient could be obtained even for pairs of species that never occurred together. For example, the Matching coefficient for *Roxania utriculus*: *Turbonilla gradata* was 98%, simply because they were so rare in the samples and therefore had numerous absences in common.

The use of Jaccard coefficients was found to express the data more convincingly (Table 6). Jaccard coefficients are always positive and in the present set of data ranged up to a maximum of 0.33. The figure of 0.15 proved to correspond to the 0.05 level of significance in representative cases. The dendrogram shown in Fig. 5 was constructed using the same data, treated by the Weighted Pair Group Average clustering technique. It is clear that there are several examples of significant similarities. Foremost among these was the association in the samples between *Bulla striata* and *Cylindrobulla fragilis* (Jaccard coefficient 0.25), between *Weinkauffia diaphana* and *Atys jeffreysi* (0.33) and between *Rhizorus acuminatus* and *Retusa* agg. (0.28). If we are to seek causal elements in these associations, we are reduced to mere speculation, and must confess that only in the first example is it possible that the association might have a trophic basis (*Bulla striata* is omnivorous, feeding both epi- and infaunally, whereas *Cylindrobulla* is a diminutive infaunal root herbivore and might itself be taken by *Bulla*). In the other examples it seems probable that the species are positively correlated with some other factor, not directly with each other. Such factors may include a common diet (these species are micro-carnivores), or a common preference for a certain grade of sediment. The latter is in most cases unlikely because poor correlations were obtained between opisthobranch species composition and sediment-type as expressed by mean grain size, % mud content, sorting, kurtosis or skewness. The section on

TABLE 6  
A matrix illustrating the affinities between species, calculated as Jaccard coefficients.

	<i>Philine aperta</i>	<i>Haminea navicula</i>	<i>Weinkauffia diaphana</i>	<i>Atys jeffreysi</i>	<i>Odostomia conoidea</i>	<i>Retusa</i> agg.	<i>Philine scabra</i>	<i>Petalifera petalifera</i>	<i>Bulla striata</i>	<i>Rhizorus acuminatus</i>	<i>Acteon tornatilis</i>	<i>Cylichna cylindracea</i>	<i>Ringicula conformis</i>	<i>Turbonilla formosa</i>	<i>Cylindrobulla fragilis</i>	<i>Retusa truncatula</i>	<i>Aglaja tricolorata</i>	<i>Turbonilla gradata</i>
<i>Philine aperta</i>	0.21																	
<i>Haminea navicula</i>	0.19	0.24																
<i>Weinkauffia diaphana</i>	0.18	0.19	0.33															
<i>Atys jeffreysi</i>	0.05	0.06	0.13	0.15														
<i>Odostomia conoidea</i>	0.13	0.13	0.13	0.30	0.17													
<i>Retusa</i> agg.	0.10	0.17	0.14	0.07	0.08	0.08												
<i>Philine scabra</i>	0.13	0.14	0.15	0.13	0.04	0.04	0.05											
<i>Petalifera petalifera</i>	0.05	0.03	0.07	0.14	0.10	0.10	0	0										
<i>Bulla striata</i>	0.13	0.11	0.12	0.32	0.10	0.28	0.10	0	0.20									
<i>Rhizorus acuminatus</i>	0	0.07	0.12	0	0.10	0.05	0.05	0.06	0	0								
<i>Acteon tornatilis</i>	0.09	0.03	0.17	0.14	0.10	0.10	0.10	0	0	0.06	0.07							
<i>Cylichna cylindracea</i>	0.09	0.07	0	0.05	0.11	0.05	0.05	0	0.14	0.07	0	0						
<i>Ringicula conformis</i>	0	0	0.04	0	0	0	0.05	0	0	0.07	0	0	0					
<i>Turbonilla formosa</i>	0.03	0.12	0.13	0.16	0.05	0.11	0.06	0	0.25	0.15	0.08	0	0	0				
<i>Cylindrobulla fragilis</i>	0.03	0.08	0.13	0.16	0.11	0.11	0	0	0.07	0.25	0	0.08	0	0	0.09			
<i>Retusa truncatula</i>	0.03	0.04	0	0	0.06	0	0.14	0.08	0	0	0.09	0	0	0	0	0		
<i>Aglaja tricolorata</i>	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Turbonilla gradata</i>	0	0	0	0	0	0.07	0	0	0	0	0	0.13	0	0	0	0	0	0
<i>Roxania utriculus</i>																		

For the 173 stations sampled, it was calculated for the six most prevalent species that joint occurrence at 7 or more sites leads to an exact probability of less than 5%, and to a Jaccard coefficient of 0.15 or more. In simple terms, a Jaccard coefficient of 0.15 or more indicates a significant probability of coexistence.

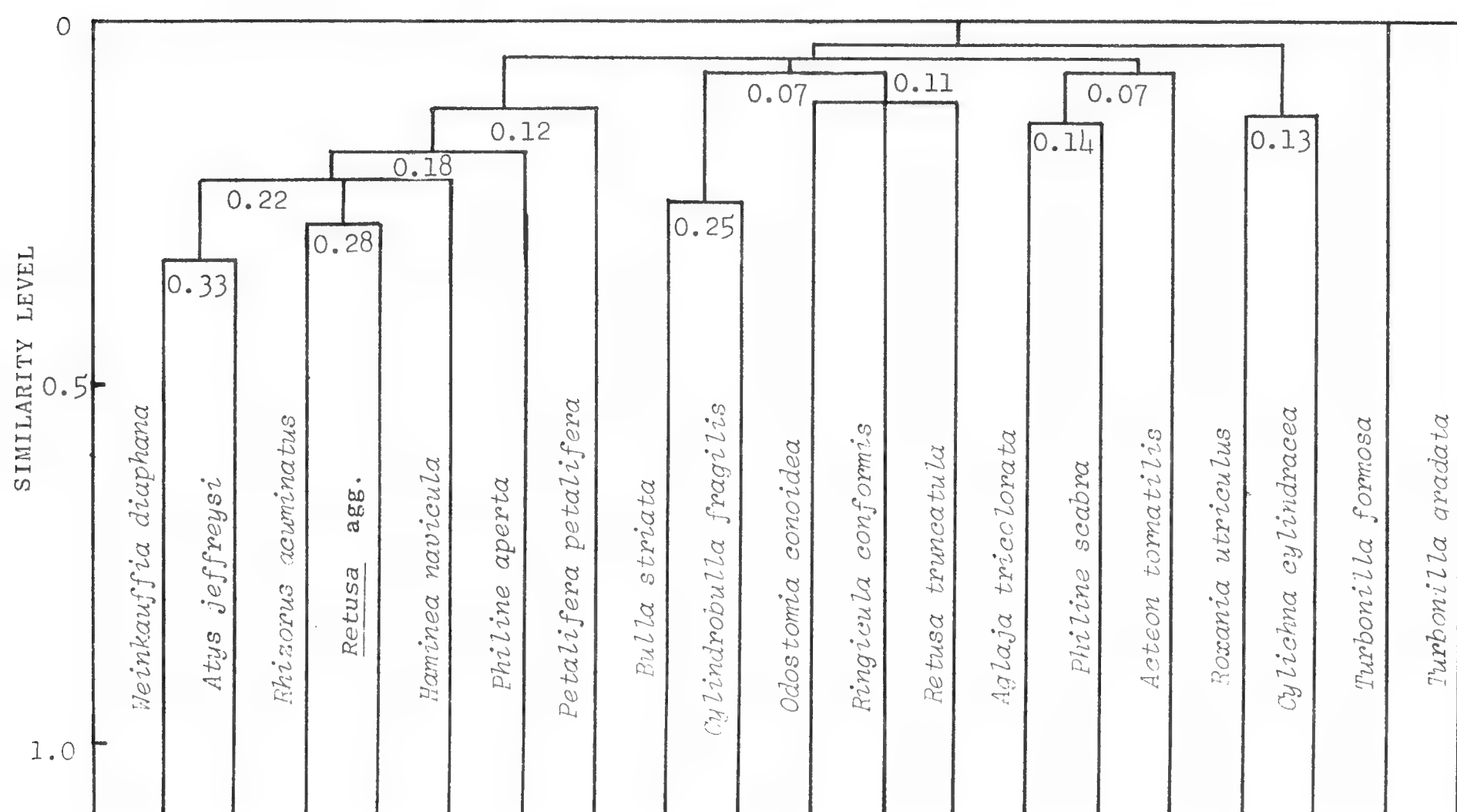


Fig. 5. Dendrogram showing the affinity between species. The fusion points were calculated from the matrix of Jaccard coefficients (Table 6) with the Weighted Pair Group Average clustering technique. A coefficient of 0.15 or more indicates a significant probability of coexistence (at the  $p < 0.05$  level).

Taxonomic and Ecological Observations includes a note of the sediment-types and % mud content for each species in turn.

#### TAXONOMIC AND ECOLOGICAL OBSERVATIONS

##### *Acteon tornatilis* (L., 1758) (Figs. 6 A & B)

This robust shell was the only operculate found in our samples. The characteristic barrel-shape of the body-whorl and the pattern of pigment-banding resembled descriptions of British specimens (e.g. Thompson 1976). The smallest specimens sometimes lacked the pigment-bands and the columellar tooth was rudimentary, but they always possessed the operculum and a radula of the *Acteon* type. This consisted of numerous similar teeth of very small size, exhibiting a number of fine subsidiary denticles. In a 2.2 mm shell the radular formula was  $40 \times 25.0.25$  and the teeth were only 5  $\mu\text{m}$  long.

Stomachs contained only thecate Protozoa (foraminiferans and radiolarians). *Acteon* occurred in substrata ranging from 2.66 to 6.55  $\phi$ , containing 0–85% mud.

##### *Bulla striata* Bruguière, 1789 (Fig. 8)

The shells of the juveniles presented marked differences from the adults (compare Figs. 8A–C), so much so that Parenzan (1970) mistakenly created a new species *Retusa mariateresae* on the basis of juveniles from Italian seas.

The smallest shells (Fig. 8A shows a 2.6 mm individual) were cream-white in colour, having a little fine sculpture (spiral striae were visible from the ventral aspect, faint growth lines on the dorsal side). The aperture was markedly longer than the spire. In a 3.5 mm shell (Fig. 8B) indistinct grey-brown blotches had developed on the outer surface of the



body whorl, and a white callus was evident. Adult shells reached 15 mm or more, and exhibited the familiar brown and white blotching overall, white callus and involute spire.

The adult radular formula was  $15 \times n.1.n$ ; all the teeth were denticulate. It was difficult to judge whether  $n = 1$  or 3 because there was some doubt about the separateness of the tooth-bases. *Bulla ampulla* (Indo-Pacific) has the formula  $n \times 1.2.1.2.1$  (Thompson 1976).

*Bulla striata* occurred in substrata varying from 2.12 to 4.37 Ø, containing 0–62% mud.

*Atys jeffreysi* (Weinkauff, 1866) (Plate 10D; Fig. 7A)

This smoothly rounded, symmetrical, robust white shell measured up to 5.25 mm in our samples. Faint striae and growth lines were detectable. The outer lip was markedly longer than the spire of the shell.

Two jaw-pads were present, bearing pointed masticatory rods. In the radula of a 4.25 mm shell, the formula was  $20 \times 4.1.4$ ; all the teeth were smooth. The 3 gizzard plates each bore 13 wrinkled transverse ridges (Plate 10D). The diet is not known, but the radula resembles the carnivorous type. *Atys jeffreysi* occurred in sediments from 1.75 to 6.36 Ø, containing 0–75% mud.

*Weinkauffia diaphana* (Aradas & Maggiore, 1840) (Plate 10C; Figs. 7B, 10I–L)

Beneath the colourless, flimsy periostracum the shell was smooth and pure white. The spire was concealed by involution, and lies in a capacious apical depression. The aperture was slightly longer than the spire. Sculpture was inconspicuous, and took the form of 7–8 spiral striae at the front and at the rear of the shell, together with sparse and very faint growth lines. There was a distinct anterior siphonal canal.

The gizzard contained 3 plates, each bearing 15 rows of masticatory bosses, up to 23 in each row (Plate 10C). Each of the ovoid plates measured approximately 225 µm in length. The plates seemed to have a replacement system, with newly formed masticatory bosses at one end, grading into worn vestiges at the other. The radula of a specimen of 2.0 mm shell-length had the formula  $n \times 3.1.3$ . The first laterals were finely denticulate but the other laterals, like the median, were smooth.

Comparative material from the Sykes collection in the British Museum (Natural History) was examined. Algerian specimens reached 4 mm in length (2.5 mm in our samples) and were slightly more broad, but were otherwise identical. This species is perhaps conspecific with Forbes' *Bulla turgidula*, and is certainly the same as *W. gibbula* (Jeffreys, 1860), according to O'Donoghue & White (1940), who described 2 specimens from Haifa.

*Weinkauffia diaphana* occurred in our samples in substrata from 1.32 to 6.55 Ø, with 0–85% mud.

*Haminea navicula* (Costa, 1778)

Several specimens were available, up to 4.25 mm in shell-length. The largest was dissected and found to be immature, lacking any trace of penis or prostate. The specimens were found in sediments ranging from 1.93 to 6.83 Ø, containing 0–88% mud.

*Ringicula conformis* Monterosato, 1877 (Figs. 6C, 10A–C)

Patras Gulf specimens did not exceed 3.5 mm in shell-length. They were smooth, robust, pure white, thick-lipped shells consisting of up to 5 whorls. The aperture was complex, having 3 columellar folds or teeth and an anterior siphonal groove.

The radula of a 3 mm shell had the formula  $n \times 1.1.1$ ; both the tiny rhachidian and the larger, hooked laterals were smooth. A pair of jaw-pads bore countless bifid or trifid masticatory elements. According to Fretter (1960) these jaw-pads are in *R. buccinea* thrust

out of the mouth during the capture of copepod and foraminiferan prey. Her description of the radula (lacking the rhachidian tooth in *R. buccinea*) disagrees with our observations on *R. conformis*.

There are many described species within the genus *Ringicula*, insufficiently distinguished from one another (Schiro 1980, Ciccone & Savona 1982). Nordsieck (1972) illustrates many species claimed for the Mediterranean fauna, but most of these fail to convince us of their separateness.

Comparative material received from Dr Simunovic of the Split Marine Institute, Yugoslavia (dredged from 10 m, 8 August 1973) proved to be similar in every respect to our *R. conformis*. In our samples, *R. conformis* occurred in sediments from 2.12 to 6.90 Ø, containing 0–91% mud and 0–62% gravel.

*Cylichna cylindracea* (Pennant, 1777) (Figs. 7D, 10D–F)

Shells up to 5 mm in length (2 mm in breadth) were found in our samples; they were dull white in colour with a tendency towards rusty or orange markings (found also in British material examined for comparison). The aperture was slightly longer than the involute spire; the shell was moderately robust. The length: breadth ratio was 2.5 or 2.6, similar to material from northern Europe examined in the British Museum (Natural History).

The jaw-elements were approximately 12 µm long and each consisted of a solid basal plate bearing a tricuspid projection (Fig. 10E). The radula of a 5 mm shell had the formula 15×4.1.1.1.4. All the teeth exhibited fine denticulations (overlooked on the lateral and marginal teeth by Lemche 1956). The gizzard plates each bore 13 elevated transverse masticatory ridges.

In the samples *C. cylindracea* occurred in substrata varying from 1.32 to 6.55 Ø, containing 0–85% mud.

*Rhizorus acuminatus* Bruguière, 1792 (Fig. 7C)

The frail white external shell reached 1.8 mm in length in our samples, 0.75 mm in breadth. A few faint growth lines were detectable. The protracted posterior siphonal canal was characteristic.

This species was found in sediments ranging from 2.0 to 4.37 Ø, with a mud content of 1 to 53%.

*Retusa truncatula* (Bruguière, 1792) (Fig. 7G)

The shell reached a length of 2.4 mm in our samples (1 mm broad). It was pure white, with faint growth lines and spiral striae. The aperture was always longer than the involute spire.

The radula was absent (as is usual in the genus) but 3 resistant gizzard plates were found, each 280 µm long, with approximately 30 dark brown masticatory bosses.

In our samples, *R. truncatula* occurred in 2.0–4.37 Ø sediments, containing 1–50% mud.

*Retusa* agg. (Plate 10A; Figs. 7F, H)

Numerous small *Retusa* spp. were found in the samples, some damaged, some resembling *R. umbilicata* (Montagu, 1803), others resembling *R. obtusa* (Montagu, 1803) and all fitting well into Milashewich's (1916) description of his *R. variabilis* from the Sea of Azov and the Black Sea. The 3 gizzard plates of a 2.5 mm shell each measured 375 µm in length. They bore a number of regular dark brown masticatory bosses which form a jumble near one end close to a terminal zone lacking any rugosities. Serial sections through two specimens showed that the ovotestis was fully mature, so these specimens are not juvenile stages of, for example, *R. truncatula*. Comparison with the Mediterranean *Retusa* species in

the collections of the British Museum (Natural History) have failed to shed light upon their true identity. The gizzard contained the remains of thecate Protozoa.

*Philine aperta* (L., 1767) (Plate 9C & D; Figs. 8D, 10H)

This pure white species is easy to recognize, with its quadripartite subdivision of the body and its flattened internal shell. It is widely distributed through the north and south Atlantic from Norway to the Cape of Good Hope.

The body shrinks after preservation so that a specimen measuring 6.3 mm in alcohol possesses a 3.8 mm shell. The radula has the formula  $n \times 1.0.1$ ; each lateral tooth bears a row of fine denticles. Our samples contained chiefly juveniles. Two individuals which measured 3 mm in alcohol had the formulae  $14 \times 1.0.1$  and  $18 \times 1.0.1$ .

This species occurred in substrata varying from 0.2 to 6.36 Ø, containing 0–79% mud.

*Philine scabra* (O. F. Müller, 1776) (Figs. 6D, 10M, N)

The preserved 2 mm long body of one specimen yielded a shell 1.75 mm in length, 1.0 mm broad. The slender shape of the white shell together with the catenate sculpture evident on close inspection are conclusive in naming this species. The radula of this individual had the formula  $n \times 1.1.0.1.1$ ; the first lateral tooth was enlarged and bore a row of fine denticles on the masticatory margin, while the 2nd lateral was smooth and slender (Figs. 10M, N).

*Philine scabra* was found in sediments from 2.8 to 6.55 Ø, containing 0–91% mud.

*Aglaja tricolorata* Renier, 1804 (Fig. 9F)

This identification was based upon shell characters; the bodies were badly contracted and all colour had faded. The internal shell was white, frail and only lightly calcified. The protoconch was smooth, without sculpture, but the dilated body whorl exhibited faint growth lines and a ridge along the outer lip. No radula, jaws or gizzard plates were found.

*Aglaja tricolorata* was associated in the samples with sediments ranging from 2.66 to 5.8 Ø, containing 0–64% mud.

*Odostomia conoidea* (Brocchi, 1814) (Fig. 6E)

In the samples, *O. conoidea* was associated with sediments ranging from 1.08 to 5.8 Ø, containing 0–66% mud. It was accompanied by *Astropecten* in two samples, corroborating the observation that it may feed upon this starfish (Fretter & Graham 1962).

*Turbonilla formosa* (Jeffreys, 1848) (Fig. 6G)

In the samples, this species was associated with sediments from 2.86 to 8.9 Ø, containing 0–10% mud.

*Turbonilla gradata* (Buquoy, Dautzenberg & Dollfus, 1883) (Fig. 6F)

This species was found in sediments ranging from 0.02 to 3.18 Ø, containing 0–5% mud.

*Petalifera petalifera* (Rang, 1828) (Plates 9B & 10B; Figs. 8E & 9C–E)

The samples contained juveniles which were poorly preserved; only the examination of the hard parts (shell, radula and jaw-plates) enabled identification. Fig. 8E shows a live, sexually mature specimen from the Saronic Gulf for comparison; details of the shell of this individual are shown in Figs. 9D & E. The usual appearance of a preserved juvenile from our infralittoral samples is shown in Fig. 9C.

In the living animal the smooth skin is pale brown with dark brown speckling over the dorsum (absent inside the parapodial lobes) and a characteristic radiating pattern of

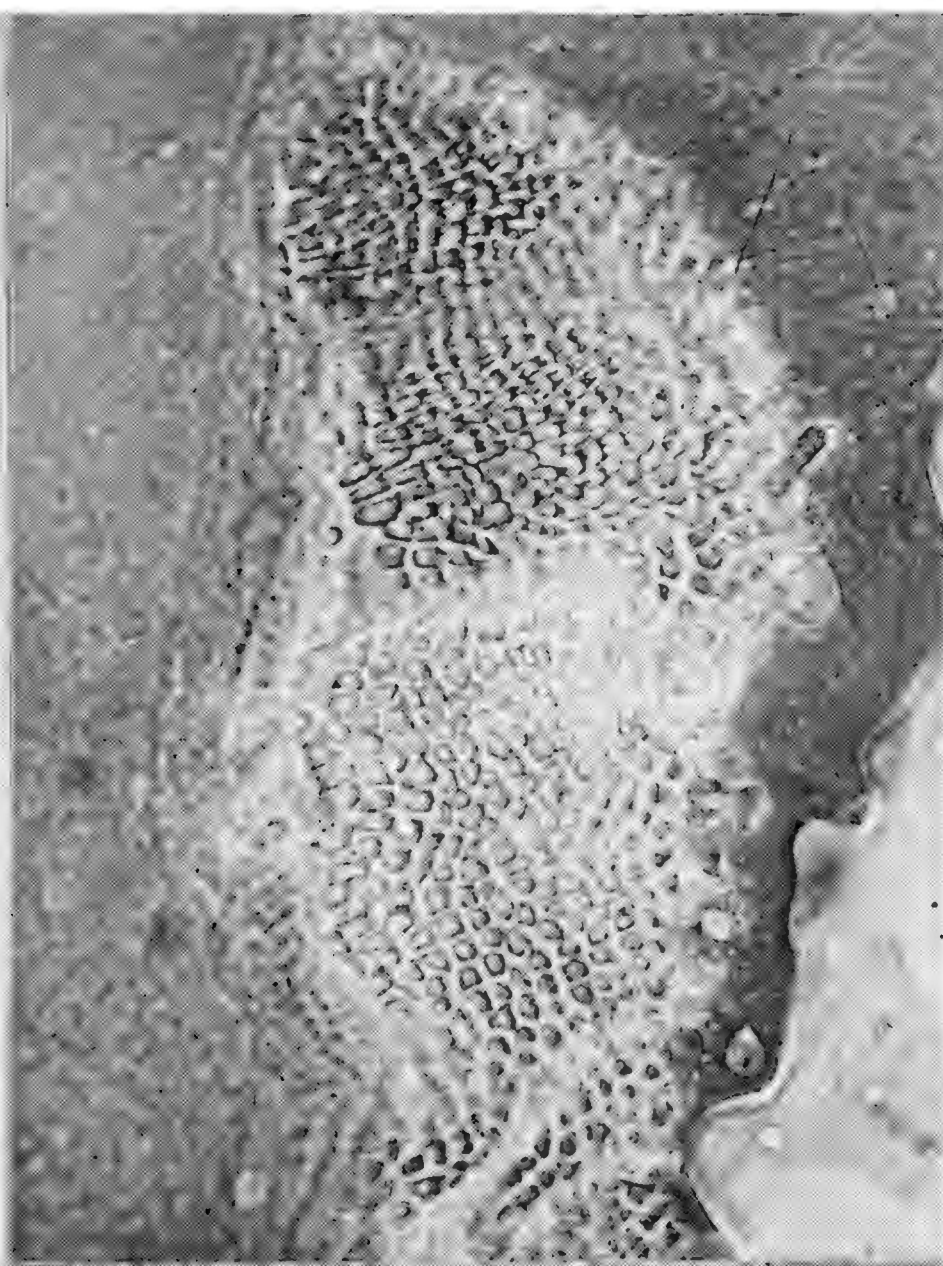


35  $\mu$ m

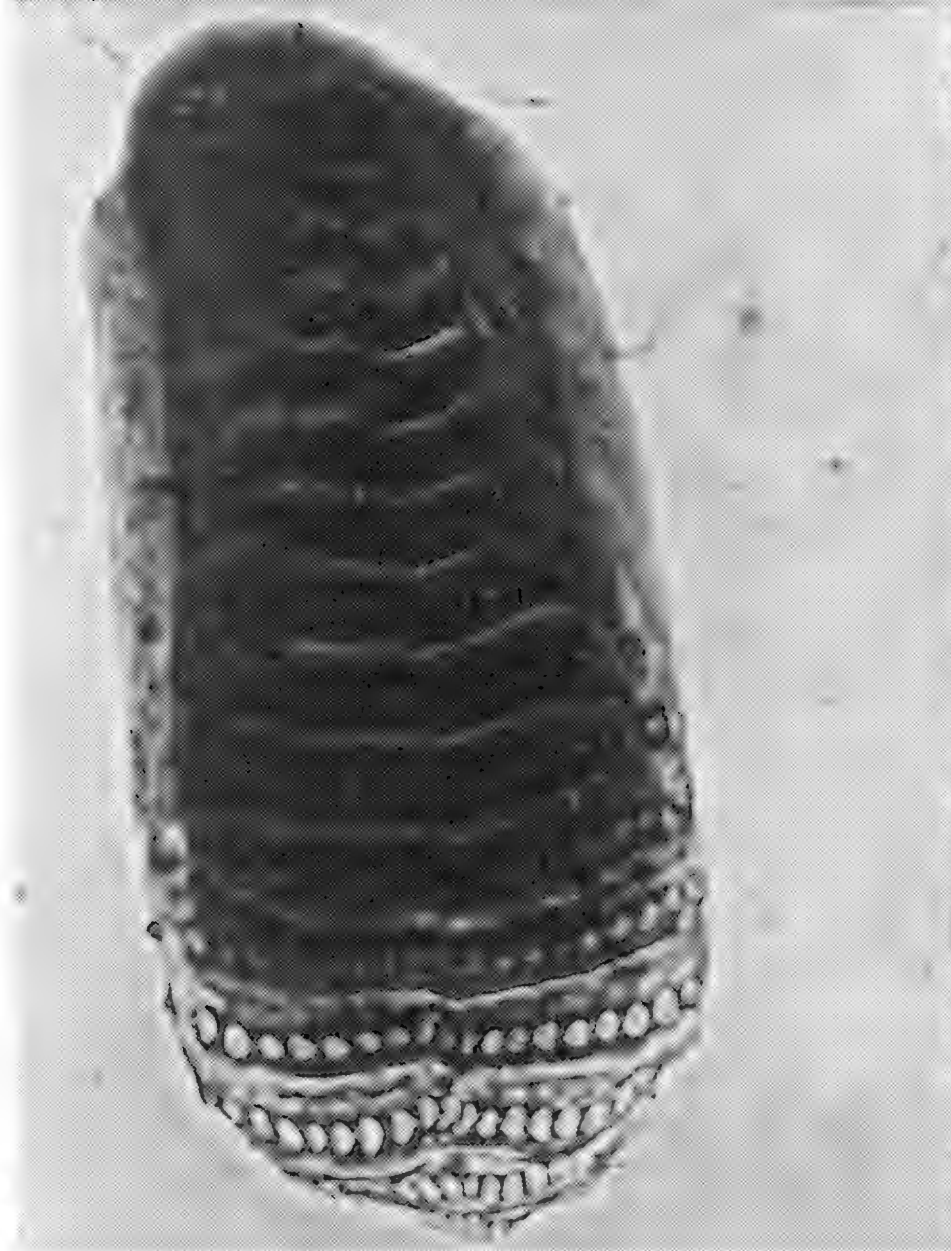
A



B



C



20  $\mu$ m

D



35  $\mu$ m

PLATE 9

Radulae of opisthobranchs.

A, *Cylindeobulla fragilis*, showing both old and new ends of the uniseriate radular ribbon; shell-length 5 mm. B, *Petalifera petalifera*, body-length 30 mm, showing central part of radula, with 5-cusped median teeth and 3-cusped laterals. C & D, *Philine aperta*, different aspects of the lateral teeth, each bearing up to 40 fine denticles; shell-length 4 mm. Phase-contrast photomicrographs.



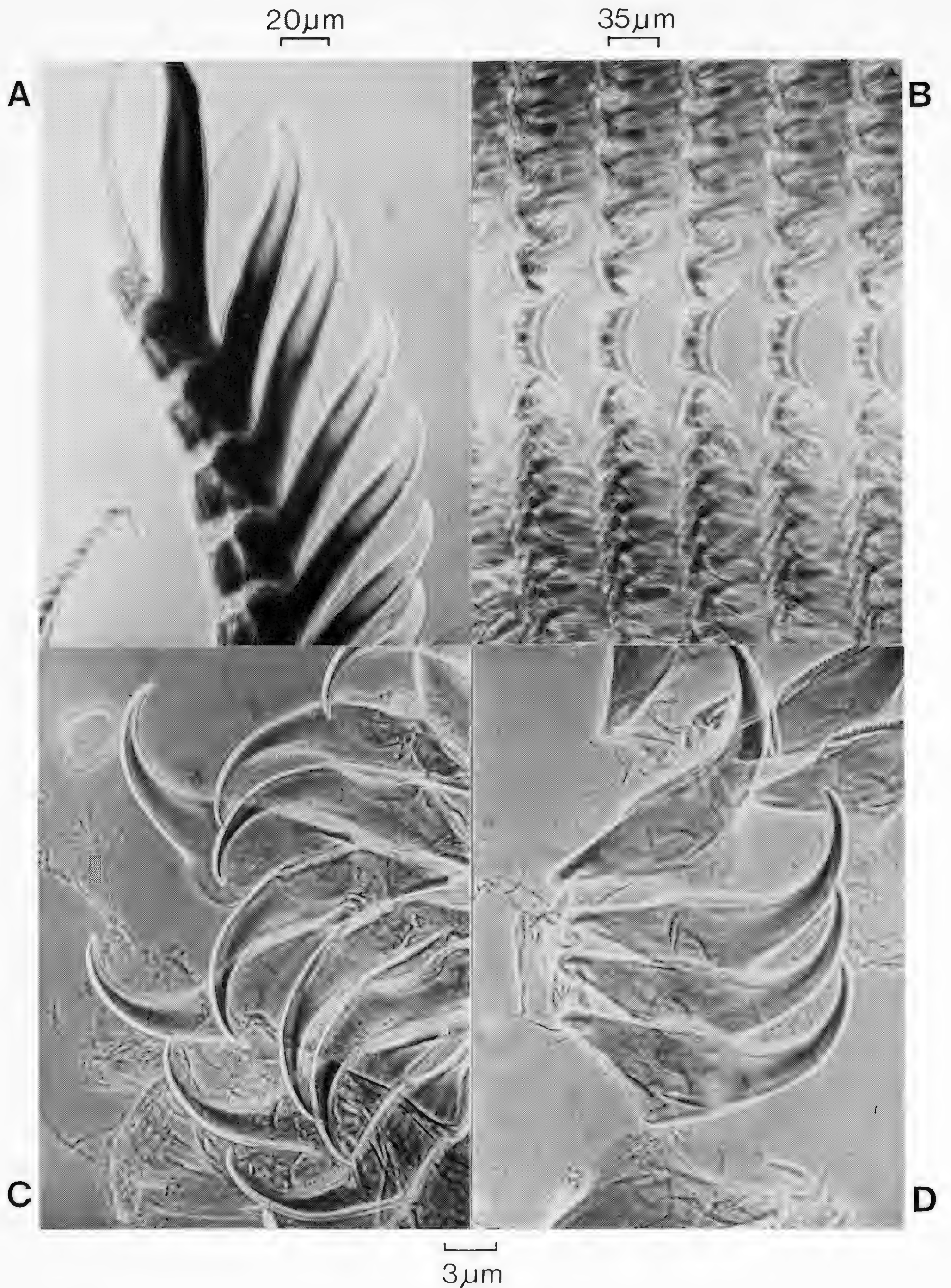


PLATE 40

Masticatory structures in the opisthobranchs.

A, *Retusa* agg., gizzard plate; shell-length 2.5 mm. B, *Petalifera petalifera*, buccal armature consisting of numerous denticulate elements; body-length 30 mm. C, *Weinkauffia diaphana*, gizzard plate; shell-length 2.0 mm. D, *Atya jeffreysi*, gizzard plate; shell-length 4.25 mm. Phase-contrast photomicrographs.



patches of white. Most of these white patches are associated with a bundle of yellow subepidermal granules, possibly defensive glands. The pedal sole is pale brown with large irregular blotches of brown, and multitudes of white spots, some quite large, usually taking the form of longitudinal streaks near the sides of the foot. A conspicuous pair of eyespots is visible in front of the bases of the inrolled rhinophores. The mantle cavity is shielded by an overlapping pair of parapodial lobes; they gape anteriorly to admit the inhalant respiratory flow and posteriorly, where a short pallial siphon directs the exhalant flow. The external autospermal groove leads from the genital opening inside the parapodial lobes to the penial opening on the side of the body, below the right rhinophore. If the parapodia are forced apart, the shell may be seen, partially ensheathed by the mantle. This shell is white and very frail (Figs. 9D & E); it is slightly concave. In the 30 mm specimen described above, the shell measured 7.5 mm in length, 5.2 mm in breadth. The body shrinks greatly on preservation so that a 7 mm long shell may be extracted from a preserved individual 11 mm long.

Fig. 9C shows a representative preserved specimen from the Patras Gulf. Details of the head are obscure but the shell (overlain by the perforate mantle epithelium) and the buccal armature are sufficient for a positive identification. It is noteworthy that the shells of such juveniles (measuring approximately one-half the body-length in preservative) exhibit a flared siphonal emargination (Fig. 9C).

The radula of a 30 mm adult had the formula  $28 \times 10.33.1.33.10$  (Plate 9B). The rhachidian teeth were 5-cusped; the laterals were stout with a spathulate cusp, becoming 3-pronged near the median plane; the marginals were smooth and slender. The buccal armature ('jaws') consisted of large numbers of denticulate units (Plate 10B).

The diet of *Petalifera* species worldwide consists of encrusting algae. Our Saronic Gulf specimen supports this; it was found under a stone in shallow water (1 m). The Patras Gulf material indicates that the juveniles spend their early lives on soft substrata. In the dredged samples, *P. petalifera* was associated with sediments 1.93–3.02 Ø, containing 0–10% mud.

*Cylindrobulla fragilis* (Jeffreys, 1856) (Plate 9A; Figs. 9A, B, 10G)

Specimens reached a shell-length of 5 mm, with a breadth of 2.5 mm. The outer lip was flexible and the aperture very narrow. The spire was concealed by the involuted growth of the body whorl. The aperture was not as long as the spire. Growth lines and spiral striae were evident on the dull white fragile shell.

The uniseriate radula of a 5 mm shell was examined (Plate 9A; Fig. 10G). The teeth formed a continuous series and there was no jumble of discarded teeth in an ascus sac. There were 11 teeth on the new limb of the radular ribbon, one tooth in the functional position, and 26 teeth on the post-functional limb. Three or 4 of the oldest, smallest teeth were smooth, but the others exhibited up to 36 slender denticles on either side of the elongated cusp. The length of the functional tooth was 155 µm, but the newest teeth measured up to 250 µm. The radular formula was  $38 \times 0.1.0$ . Each tooth had a subterminal recess into which the tip of the preceding tooth fitted.

This species is often associated with *Caulerpa prolifera* (Fasulo *et al.* 1982) and it may be postulated that, like *Volvatella* (Thompson 1979), it feeds on the roots of this alga. In the dredged samples, *C. fragilis* was associated with sediments of 3.62–4.37 Ø, containing 35–60% mud.



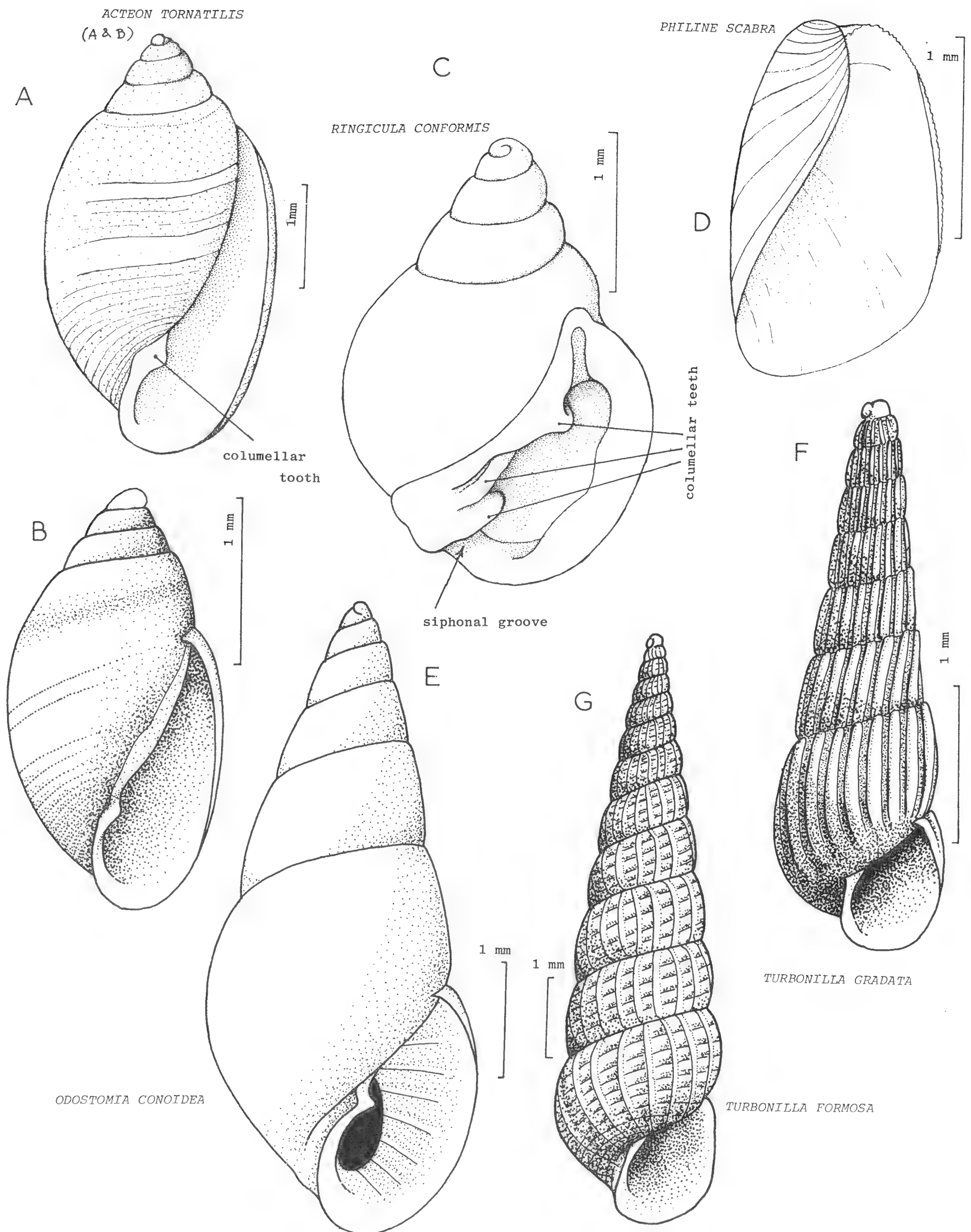


Fig. 6. Opisthobranchs from the samples.

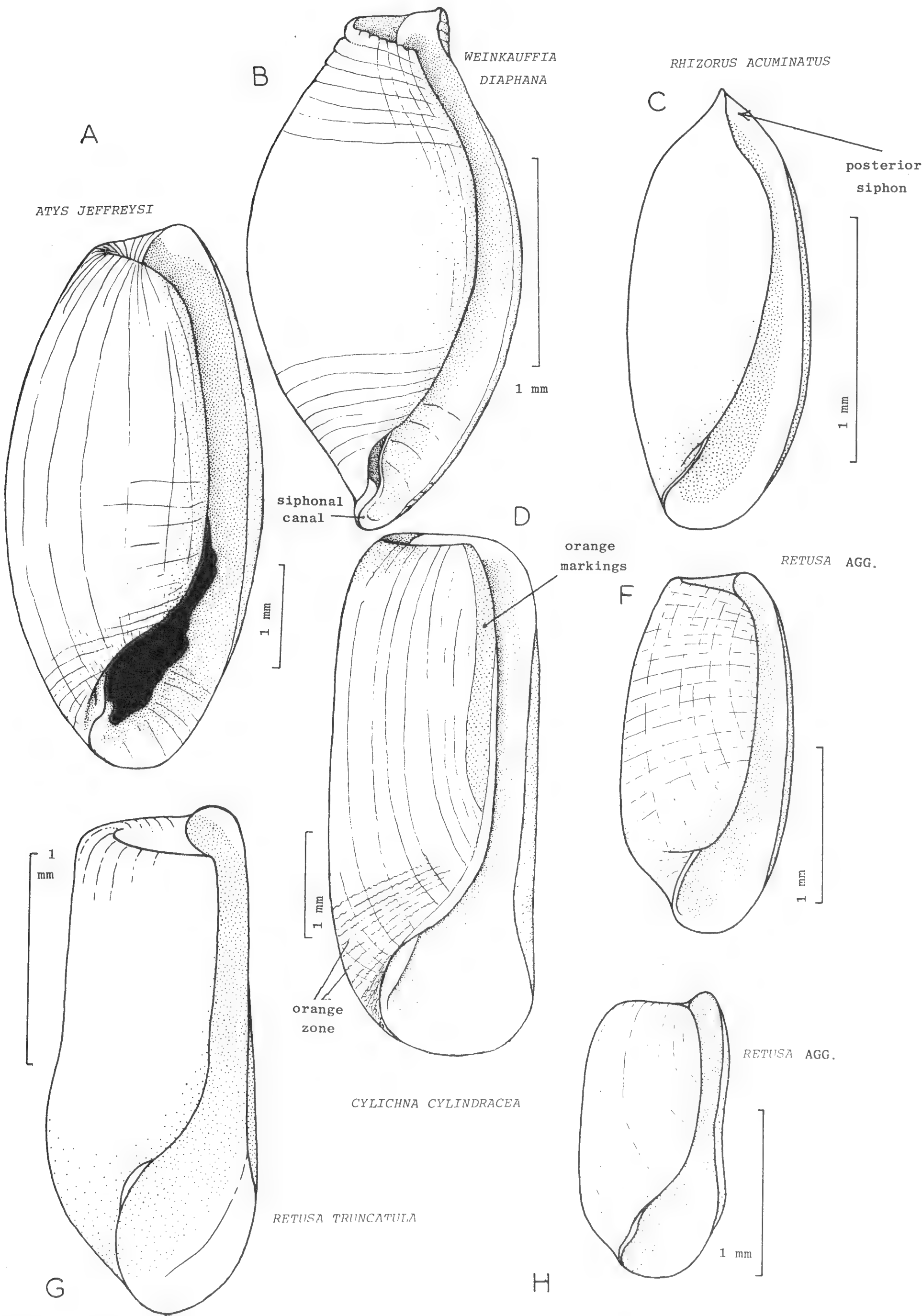


Fig. 7. Opisthobranchs from the samples.

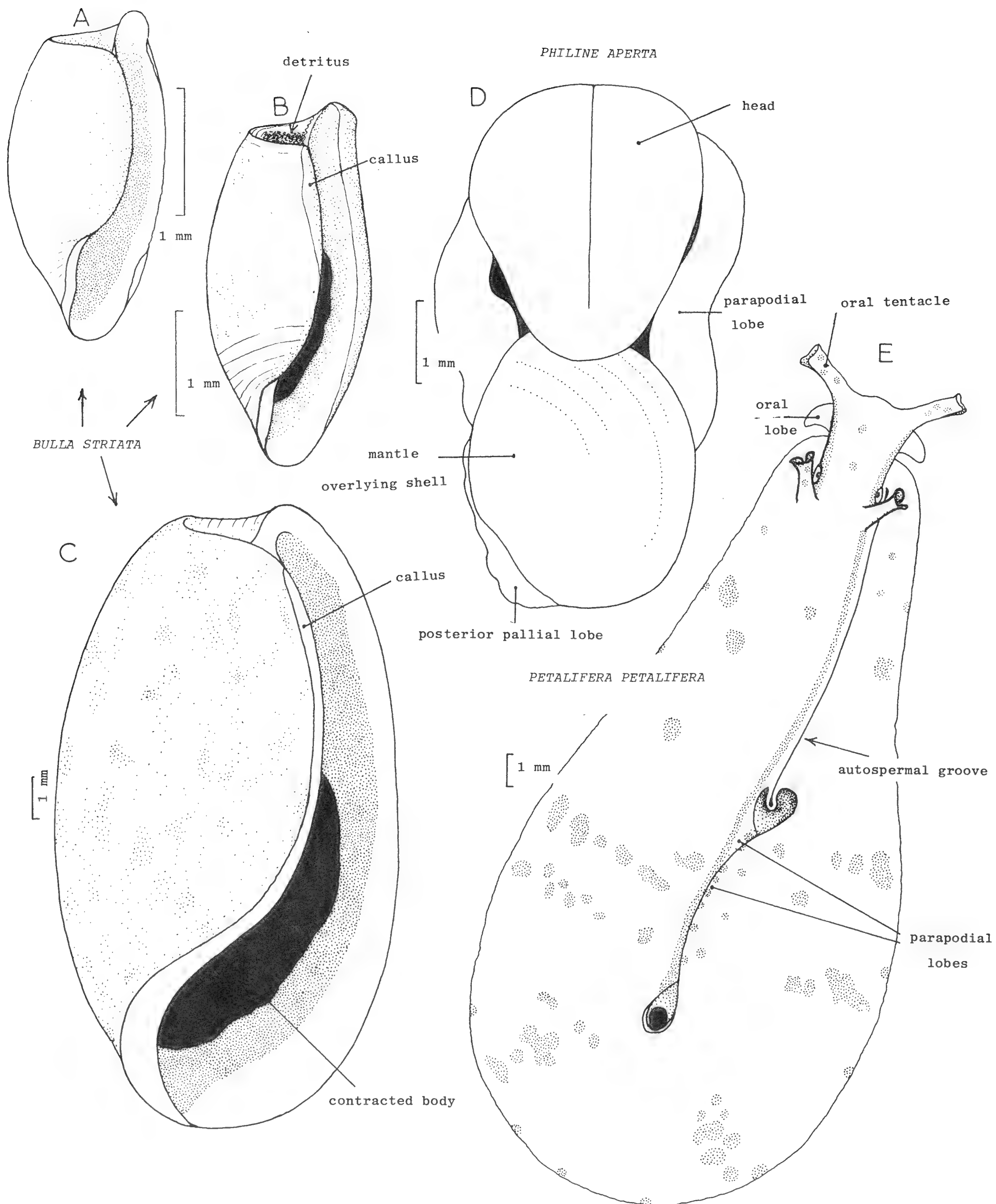


Fig. 8. Opisthobranchs from Greek waters; E is from the Saronic Gulf, others from the samples.



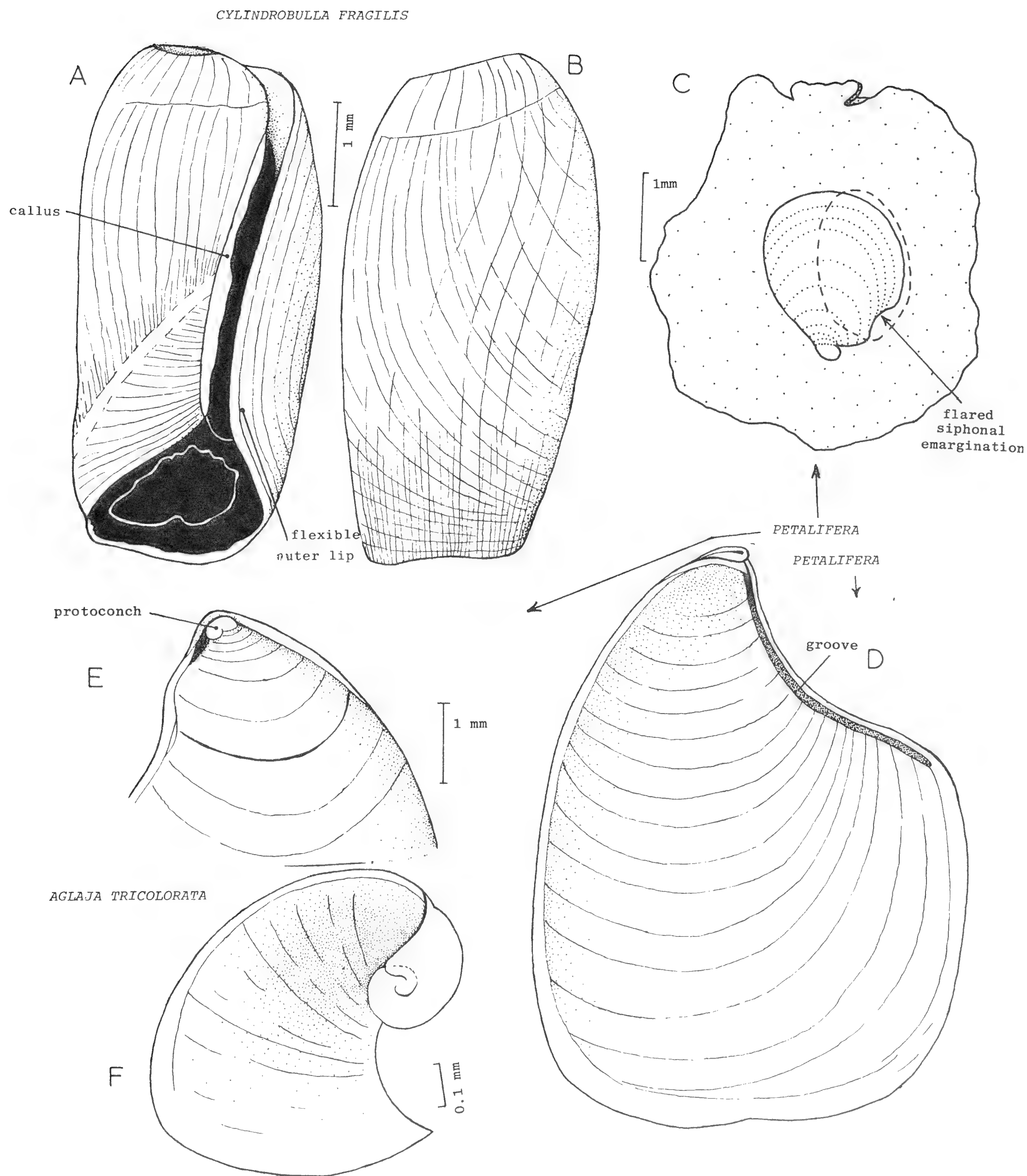


Fig. 9. Opisthobranchs from Greek waters; D & E are from the Saronic Gulf, others from the samples. In C the interrupted line delimits the pallial opening over the mainly internal shell.

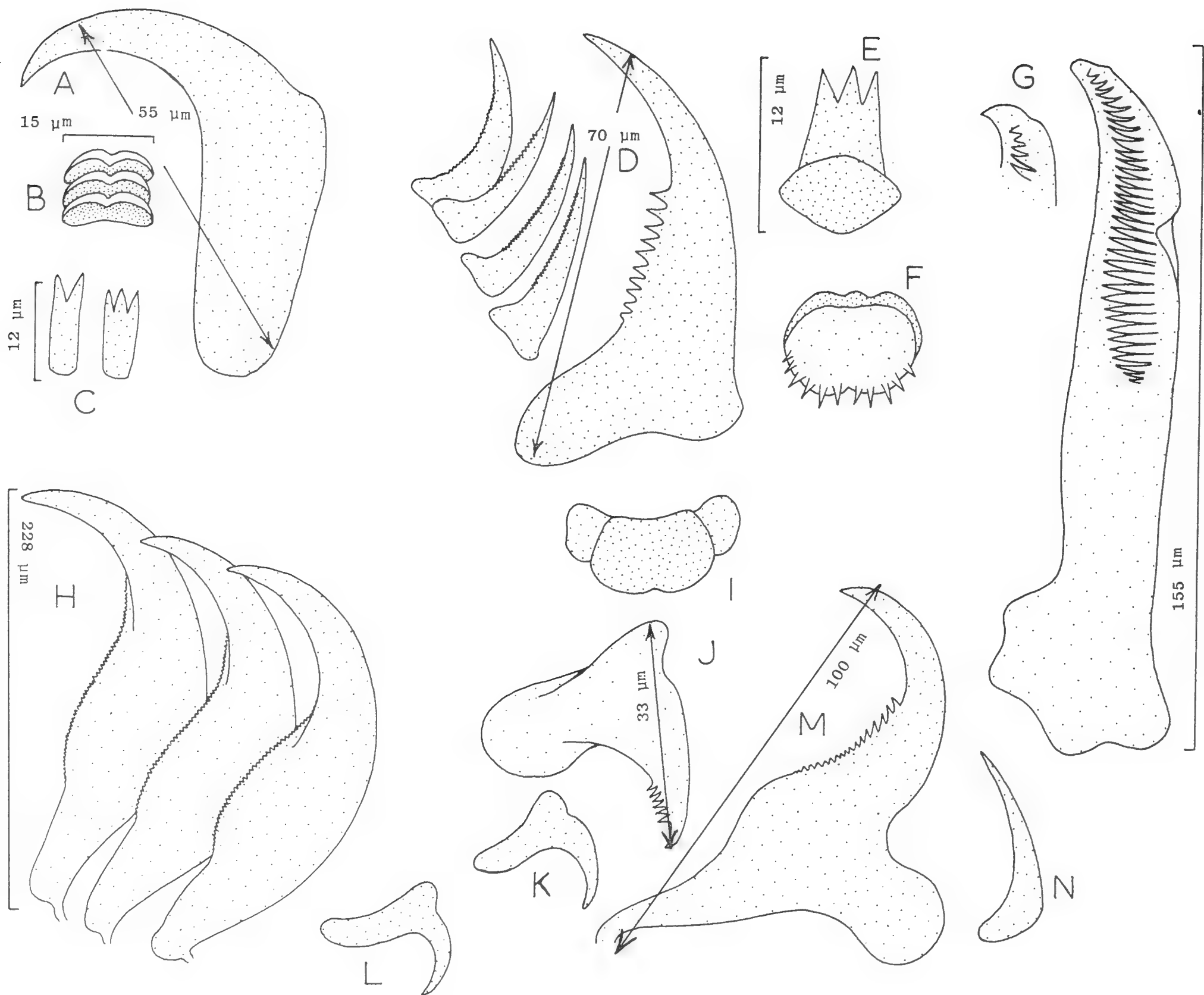


Fig. 10. Radulae and jaws of opisthobranchs. A–C, *Ringicula conformis* shell-length 3 mm, A, lateral radular tooth, B, three median teeth, C, jaw elements. D–F, *Cylichna cylindracea* shell-length 5 mm, D, lateral teeth from one half-row, E, jaw element, F, median tooth, same scale as D. G, *Cylindrobulla fragilis* shell-length 5 mm, common alternative tip-shapes depicted. H, *Philine aperta* shell-length 4.0 mm, three successive half-rows depicted. I–L, *Weinkauffia diaphana* shell-length 2.0 mm, I, median radular tooth, J, first lateral teeth, K & L, second and third lateral teeth. M & N, *Philine scabra* shell-length 1.75 mm, M, denticulate first lateral tooth, N, smooth second lateral, camera lucida drawings from polyvinyl-lactophenol preparations.

## DISCUSSION

Little is known about the prevalence of macrobenthic opisthobranchs, less still about the sublittoral forms, and least of all about infaunal species. The present infralittoral surveys go some way towards filling the need for quantitative information, but they have the defect that they were conducted over a short period of time in the summers of 1981 and 1982. With the limited manpower presently available, this was inevitable. Despite these restrictions, the opisthobranchs recorded were unprecedentedly varied; these are the most varied assemblages of infaunal and epifaunal opisthobranchs yet reported in the Mediterranean Sea or anywhere else. This rich infralittoral fauna prompted questions about possible ecological interactions, and a search was made for evidence of clustering or community-formation. Was the prevalence of the opisthobranch species governed solely by

abiotic factors—(such as a shared preference for a particular grade of bottom-deposit), or were conjoint presences due to inter-specific interaction (such as a predator-prey relationship)?

Analyses of the data for the 19 opisthobranch species obtained in the infralittoral samples revealed only three significant correlations. Of these three, only one, between *Bulla striata* and *Cylindrobulla fragilis* (both infaunal species) has a possible trophic basis, in that the omnivorous *Bulla* is capable of ingesting *Cylindrobulla*. In all the remaining examples, there was a strong indication that prevalence of opisthobranch species was correlated with a complex mixture of abiotic factors, such as depth (especially important for the herbivorous species) and grade of deposit. But there is a difficulty in placing any reliance upon the latter factor, because many infralittoral opisthobranchs were found in samples of varied mud-content and sediment-type. Such perplexities are probably inevitable in restricted sampling programmes carried out in one season of the year. To identify abiotic limiting factors will need a protracted programme of macrobenthos sampling.

The study-area proved to contain opisthobranch species of varied biogeographical and biohistorical categories. The majority were stable, widely distributed, well established Mediterranean forms. There were no Ionian Sea endemics, nor were there any Indian Ocean forms which had immigrated via the Suez Canal and the Red Sea. Such infralittoral conservatism contrasts with innovations recorded for the epifaunal opisthobranchs of hard bottoms in the Ionian and Aegean Seas. For example, recent investigations have documented the epifaunal (occasionally pelagic) opisthobranch *Melibe fimbriata* (Thompson & Crampton 1984), a Lessepsian immigrant, previously known only from Ceylon; *Hypselodoris webbi* and *Elysia flava* (amphiatlantic species from Bermuda, Florida and the Canary Islands) are other cases of spectacular range-extension (Thompson 1983, Thompson & Turner 1983). These facts point to the conclusion that resource-partitioning is more complete and mature in the infralittoral benthos of the study-area than in the under-exploited hard bottoms of adjacent areas of the eastern Mediterranean. Por (1971) suggested that the eastern Mediterranean was 'pre-adapted' to receive tropical immigrants because there were many niches vacant. It seems likely, however, that this applies more to animals of the pelagic and epibenthic environments than to the macrobiota of soft bottoms.

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# ABYSSAL MOLLUSCA OF THE ARCTIC OCEAN

JØRGEN KNUDSEN<sup>1</sup>

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*Abstract:* The mollusc material of the FRAM I Drift-Ice Expedition 1979 consists of 13 species, mostly represented by shells without the soft parts. Two new taxa were present: *Yoldiella frami* n.sp. and *Cuspidaria* sp., apparently new but material too damaged for an adequate description. An attempt has been made to compile a checklist of all known molluscs from the arctic abyssal zone, i.e., deeper than 1200 meters. Altogether 36 taxa have been recorded (18 Gastropoda, 1 Scaphopoda, 17 Bivalvia). The horizontal and vertical distribution of the taxa are recorded. The earlier observation that the Norwegian Sea and the Arctic Ocean form a zoogeographical unit is confirmed. An endemic abyssal faunal element can be recognized. Observations on mode of life (attachment) and feeding lead to the conclusion that the arctic abyssal zone contains a number of ecological niches.

## INTRODUCTION

The present study deals with the molluscs collected in May 1979 during the dredging operations of the US-Canadian-Norwegian-Danish drift-ice station FRAM I, working off northeast Greenland at depths between 2300 and 3900 meters. Dr. Jean Just of the Zoological Museum of Copenhagen was in charge of the dredging operations. Ten species of bivalves and 3 species of gastropods were obtained, mostly represented by shells without the soft parts. Altogether about 750 shells, but only 6 specimens with the soft parts preserved, were dredged from 8 stations. Just (1980) should be consulted for details of the expedition. A few samples from other sources are included in the present study. The collection is kept in the Zoological Museum of the University of Copenhagen.

Just (1980) tentatively put the limit between the Arctic Ocean and the Norwegian Sea in the Fram Strait at 80°N.

Bouchet & Warén (1979) studied the molluscs collected in 1975 by the Swedish-French NORBI expedition in the Norwegian Sea; about 90,000 'live' specimens were obtained from 11 stations at depths between 2500 to 3700 meters. The authors presented a survey of earlier investigations of the molluscs of the arctic abyssal; besides describing 5 new species, they undertook a systematic and taxonomic revision of nearly all species known from the arctic abyssal zone. They also gave a complete synonymy for each species, summarized all earlier records of the species and gave excellent figures of the species they studied. Throughout the present paper reference is made to that of Bouchet & Warén.

## SYSTEMATIC ACCOUNT

### Gastropoda

*Lissospira turgida* (Odhner, 1912).

*Lissospira turgida*.—Bouchet & Warén 1979, p. 221, Figs. 37–39.

*Material:* St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 1 shell.

<sup>1</sup> Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.

*Remarks:* The present shell agrees very well with the original description and the figures in Bouchet & Warén (1979).

*Distribution:* Previously known only from the Norwegian Sea, the present material is the first record from the Arctic Ocean. Vertical range of live specimens: from about 2700 to 3670 m.

*Pseudosetia semipellucida* (Friele, 1879).

*Pseudosetia semipellucida*.—Bouchet & Warén 1979, p. 222, Fig. 42.

*Material:* St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 1 shell.

*Remarks:* The shell agrees well with the figure in Bouchet & Warén (1979); the two authors studied the type of this hitherto unfigured species.

*Distribution:* Previously known only from the Norwegian Sea, the present shell is the first record from the Arctic Ocean. The vertical range is from about 2500 to about 3200 m.

*Mohnia mohni* (Friele, 1877)

*Mohnia mohni*.—Bouchet & Warén 1979, p. 226, figs. 14 A–B, 48, 50.

*Material:* St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 1 shell.

St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 9 shells, fragments.

*Distribution:* Numerous records from both the Norwegian Sea and the Arctic Ocean. The vertical range of live specimens is from about 1100 to between 3350 to 3670 m.

## Bivalvia

*Nucula zophos* Clarke, 1960

*Nucula zophos*.—Clarke 1960, p. 5, Pl. 1, Figs. 15–18; Clarke 1963, p. 99; Paul & Menzies 1973, p. 127; Bernard 1979, p. 11, Fig. 2.

*Material:* St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 16 valves, some broken.

*Remarks:* The present valves exhibit the elongate shape, the reticulate sculpture and the crenulate edge shown in the figures of the species. The smaller valves, less than 4 mm long, have 6–10 anterior and 3–4 posterior hinge teeth. The larger valves, 11–13 mm long, have about 15 anterior teeth; owing to damage the number of posterior hinge teeth could not be ascertained. The prodissoconch has a diameter of about 350  $\mu$ m.

*Distribution:* *Nucula zophos* was described from single valves from the northern part of the Alpha Cordillera, about 800 miles north of Point Barrow, Alaska; subsequent records from the Chukchi Plateau, about 800 miles north of Bering Strait, included live specimens (Clarke 1963); Bernard (1979) recorded valves from the Beaufort Sea.

The known vertical distribution of living specimens is from 530 to 2237 m.

*Tindaria derjugini* Gorbunov, 1946.

*Tindaria derjugini*.—Bouchet & Warén 1979, p. 212, Figs. 1, 25, 26;

*Malletia abyssopolaris*.—Bernard 1979, p. 12, Fig. 5.

*Material:* 1 May, 84°10'38"N, 7°48'52"W, clay in hydrophone, 3620 m, 4 valves.

St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 38 valves.

St. 15, 84°00'25"N, 7°16'40"W, 3500 m, 1 valve.

St. 17, 83°48'32"N, 6°50'25"W, 3000 m, 2 valves.

St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 25 valves.

*Remarks:* Bouchet & Warén (1979) summarized known records of the species and synonymized *M. abyssopolaris* Clarke, 1960 with *T. derjugini*.

*Distribution:* The species is widely distributed in the Arctic Ocean and the Norwegian Sea. Live specimens are known from several localities around a depth of 2500 m. Valves are known from depths ranging from about 1500 to 2300 m.

*Katadesmia kolthoffi* (Hägg, 1904)

*Katadesmia kolthoffi*.—Bouchet & Warén 1979, p. 214 Figs. 2A–C, 21, 22.

*Material*: 1 May, 84°10'38"N, 7°48'52"W, Clay in hydrophone, 3620 m, 15 valves.

St. 1, 84°19'38"N, 8°19'06"W, 3930 m, 3 spec.

St. 3, 84°19'1" N, 8°15'2" W, 3500 m, 64 valves.

St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 185 valves

St. 12, 84°13'38"N, 7°56'51"W, 3965 m, 12 valves.

St. 15, 84°00'25"N, 7°16'40"W, 3500 m, 2 valves.

St. 17, 83°48'32"N, 6°50'25"W, 3000 m, 4 valves.

St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 3 valves.

*Remarks*: The status of the species was discussed by Bouchet & Warén (1979), who also gave excellent figures of it.

*Distribution*: Bouchet & Warén (l.c.) summarized earlier records and added a number of new ones, all from the Norwegian Sea and the Arctic Ocean. Live specimens are known from depths ranging from about 2500 to 3930 meters.

***Yoldiella frami*** n.sp. Fig. 1.

*Material*: St. 3, 84°19'1" N, 8°15'2" W, 3500 m, 21 valves.

St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 38 valves.

St. 12, 84°13'38"N, 7°56'51"W, 3965 m, 2 broken valves

St. 15, 84°00'25"N, 7°16'40"W, 3500 m, 3 valves.

St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 12 valves.

*Diagnosis*: A *Yoldiella* having a low spire and a strongly curved ventral edge.

*Description*: The valve is strongly compressed delicate and inequilateral; the umbo is low, the postumbonal part forming 57–61% of the total length. In lateral view the anterodorsal edge is slightly convex, while the posterodorsal edge is nearly straight; the two edges form an angle of about 160°. The posterior edge is rounded and the ventral edge is strongly curved, the greatest height of the valve being slightly posterior to the umbo. The exterior has a fine commarginal striation. Lunula and escutcheon are absent. The interior is lustrous. The indistinct pallial sinus is broad and shallow; the adductor scars are very indistinct. The ligament is very delicate. The hinge is frail and only slightly stouter towards its distal ends. The resilium is trapezoidal and deeply impressed.

Measurements and counts of right valves from St. 4:

No.	Length	mm		H/L	Postumbonal %	No. hinge teeth	
		Height	Breadth			anterior	posterior
1	6.4	4.1	1.2	0.64	59.1	7	11
2	7.4	4.7	1.4	0.64	57.1	13	15
3	7.9	4.7	1.3	0.60	58.3	13	13
4	7.9	4.8	1.3	0.61	59.7	12	12
5	7.9	4.8	1.5	0.61	57.9	13	15
6	8.5	5.0	1.6	0.59	59.4	11	15
7	8.6	5.3	1.6	0.62	58.4	14	15
8	8.7	5.6	1.7	0.64	57.2	13	17
9	9.5	5.6	1.7	0.59	58.4	12	15
10	10.3	6.1	1.6	0.59	61.1	13	16

The prodissoconch has a diameter of about 300  $\mu$ m.

*Remarks*: The present species resembles *Portlandia subequilatera* (Jeffreys, 1879). The latter is a panarctic-boreal species, which descends into the abyssal zone in the North Atlantic. Ockelmann (1958) discussed the species and gave an excellent figure of it. The present



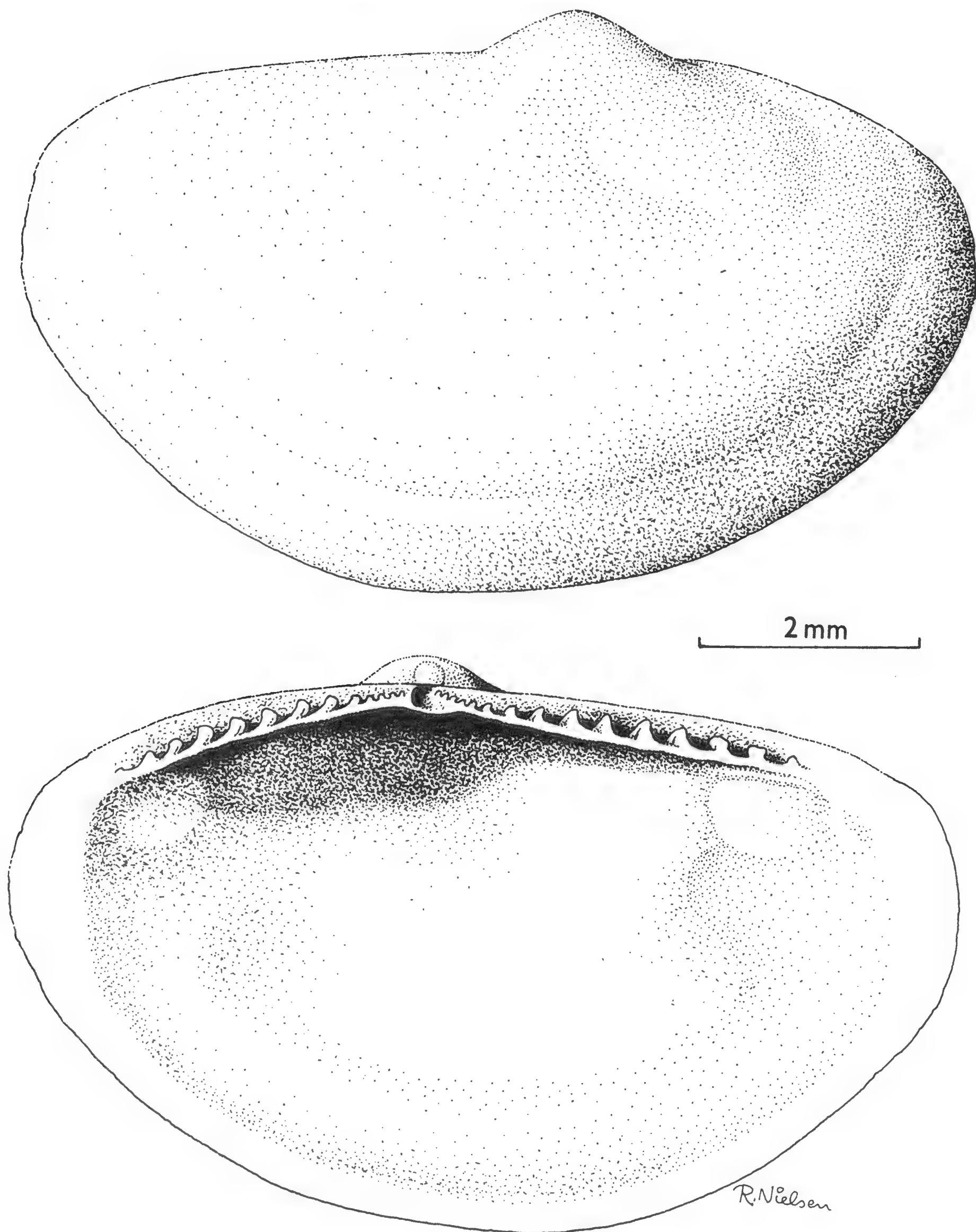


Fig. 1. *Yoldiella frami* n.sp. Exterior and interior of the type (right valve).

material has been compared with the specimens treated by Ockelmann. *Y. frami* differs by having a more delicate valve, a more rounded posterior end, a more strongly curved ventral edge, and a larger angle between the preumbonal and the postumbonal edges (which is about  $140^\circ$  in *P. subequilatera*). *Y. frami* also resembles two abyssal species from the Atlantic described by Knudsen (1970) viz., *Y. clarkei* and *Y. sootryeni*: However, these differ markedly from *Y. frami* in shape and hinge structure. In the absence of the soft parts the assignment to genus remains uncertain.

*Type:* A right valve from FRAM st. 4.

*Bathyarca frielei* Jeffreys in Friele, 1879

*Bathyarca frielei*.—Ockelmann 1958, p. 42, Pl. 1, Fig. 17; Bouchet & Warén 1979, p. 215, Figs. 29–30.

*Bathyarca raridentata*.—Bernard 1979, p. 23, Fig. 31.

*Material:* St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 300 valves.

*Remarks:* Bernard 1979 studied material of the Pliocene *B. raridentata* (Wood, 1840) and suggested that *B. frielei* would prove to be a synonym of *B. raridentata*. His description and figure, based on specimens from the Beaufort Sea shelf, agree with *B. frielei*.

*Distribution:* Known records were summarized by Bouchet & Warén (1979). The species is widely distributed in the Arctic Ocean and the Norwegian Sea.

The vertical range of live specimens is from about 20 to 2500 m.

*Hyalopecten frigidus* (Jensen, 1904)

*Hyalopecten frigidus*.—Bouchet & Warén 1979, p. 216, Figs. 31, 32.

*Material:* St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 1 valve.

*Distribution:* Bouchet & Warén (1979) summarized the known records and added many new ones. The species is widely distributed in the Arctic Ocean and the Norwegian Sea.

The vertical range of live specimens is from about 1090 to over 3000 m.

*Thyasira* sp.

*Thyasira* sp.n.—Bouchet & Warén 1979, p. 216, Fig. 4.

*Material:* St. 3, 84°19'1" N, 8°15'2" W, 3500 m, 2 valves.

St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 2 valves.

St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 26 valves.

*Remarks:* The present valves agree very well with the figure given by Bouchet & Warén (1979) and stated to represent an undescribed species.

*Distribution:* The species was hitherto known only from the Norwegian Sea; the present find extends the distribution to the Arctic Ocean.

*Policordia jeffreysi* (Friele, 1879).

*Policordia jeffreysi*.—Bouchet & Warén 1979, p. 216, Fig. 4.

*Lyonsiella* (*Policordia*) *uschakovi*.—Bernard 1979, p. 63, Fig. 109.

*Material:* St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 2 valves.

'Ingolf' Expedition St. 104, 63°23'N, 7°25'W, 1802 m, 11.7.1896, 1 juv. specimen.

'Ingolf' Expedition St. 112, 67°57'N, 6°44'W, 2386 m, 20.7.1896, 1 specimen.

'Ingolf' Expedition St. 113, 69°31'N, 7°06'W, 2465 m, 21.7.1896, 3 specimens (2 ad., 1 juv.).

'Ingolf' Expedition St. 120, 67°29'N, 11°32'W, 1666 m, 25.7.1896, 1 juv. specimen.

USNS "Lynch" Cruise, 71°28.3'N, 9°52.8'W, 2085 m, 26.9.1973, 1 specimen.

*Remarks:* Bouchet & Warén (1979) were probably correct in synonymizing *Lyonsiella uschakovi* Gorbunov, 1946 with *P. jeffreysi*; Bernhard (1979) considered the former separate, endemic to the deeper parts of the Canada Basin. Bouchet & Warén (1979) doubted that the single specimen studied by Allen & Turner (1974) belonged to *P. jeffreysi*; it was collected in the western Atlantic at about 39°38'N and a depth of 2862 m; it has 28 siphonal tentacles and a strong byssus; Bouchet and Warén's specimens had 22–24 tentacles, and no byssus was observed although the presence of a small byssus gland was noticed. The present specimens had 22–24 siphonal tentacles and a fine single-thread byssus was observed in smaller specimens. the largest specimen ('Lynch', 25 mm long) contained ripe eggs with a diameter of 200  $\mu$ m.

*Distribution:* The distribution was summarized by Bouchet & Warén (1979) who stated that the species occurs in the abyssal parts of the Norwegian Sea and the Arctic Ocean. Records from the abyssal North Atlantic are possibly due to misidentifications.

The vertical range of live specimens is from about 1600 to about 3700 m.

*Cuspidaria centobi* Bouchet & Warén, 1979.

*Cuspidaria centobi*.—Bouchet & Warén 1979, p. 218, Figs. 6, 7.

*Material:* St. 4, 84°19'00"N, 8°13'00"W, 3300 m, 1 spec.

St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 1 spec.

*Remarks:* The species was described from the Norwegian Sea where it was found at many stations, often in large numbers.

*Distribution:* The Norwegian Sea and the Arctic Ocean; the vertical range is from 2300 to about 3700 m.

*Cuspidaria* sp. Plate 11.

*Material:* St. 18, 83°40'08"N, 6°49'21"W, 2300 m, 2 valves.

*Description:* The valves are slightly inequilateral, the postumbonal part forming 53% of the total length. The valves are solid and somewhat inflated. The posterior projection is short and compressed; the umbo is rather large and the ventral edge is strongly convex. The external sculpture consists of rather regular sharp, commarginal ridges which gradually become less distinct and more irregular towards the periphery. The resilifer is small and deeply impressed; no hinge teeth are present. The adductor scars are distinct and nearly circular.

*Measurements:*

	mm				
	Length	Height	Breadth	H/L	B/L
	11.9	9.3	4.5	0.78	0.38
	10.9	8.7	4.9	0.80	0.45

*Remarks:* The two valves seem to differ from those of any other species of cuspidariid known from the region or from the North Atlantic. The species may therefore be new. However, since the valves are both rather damaged, formal establishment of a n.sp. should be postponed until better material is available.

#### GENERAL REMARKS

The limitation of the abyssal zone of the arctic seas was discussed by Bouchet & Warén (1979). They concluded that the deep area north of the Shetland-Faroe Ridge, the Denmark Strait, the northern sill of Baffin Bay and the Bering Strait constitutes a single zoogeographical unit. They also concluded that the upper limit of the abyssal fauna might be put at a depth of about 1200 m, but that it appears to be at different depths in different parts of the area; the authors stress the uncertainty of their conclusions, due to the scanty data available. They state that the arctic abyssal mollusc fauna shows a high degree of endemism, 83%, at the specific level.

In the following table an attempt has been made to compile a list of all molluscs recorded from depths greater than about 1200 m in the arctic seas. The following papers have been consulted: Bernard (1979), Bouchet & Warén (1979), Clarke (1960, 1963), Friele (1882, 1886), Gorbunov (1946 a,b), Hägg (1904, 1905), Jensen (1912), Knipowitsch



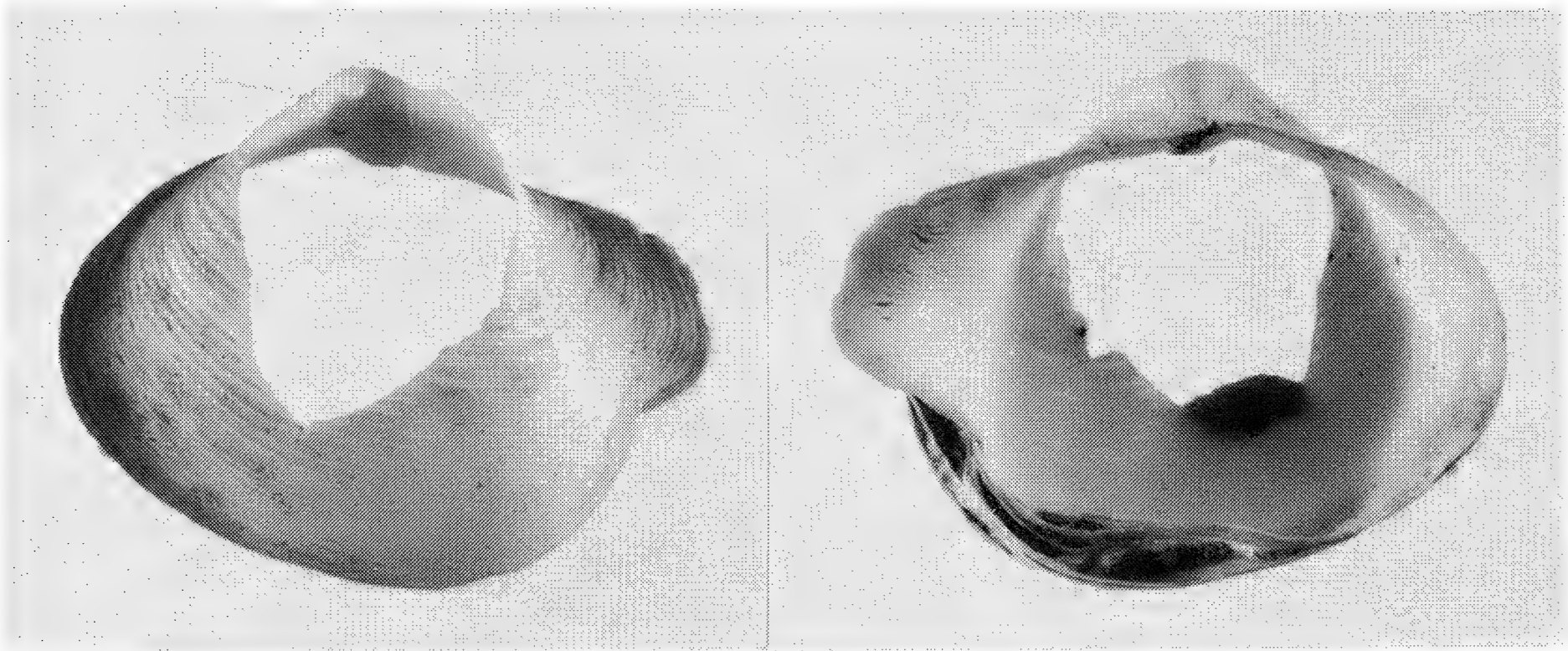


PLATE 11

*Cuspidaria* sp. Exterior and interior of a left valve. The ventral edge is double, the interspace having some partitions; the anomaly is probably due to repair of the valve after a damage.  $\times 5$ .



KNUDSEN: ARCTIC ABYSSAL MOLLUSCA

(1901), Ockelmann (1959), and Odhner (1912, 1913); For the most part only records of specimens stated to be alive at the capture have been considered.

TABLE 1

Checklist of molluscs recorded from the abyssal zone (below 1200 m) of the arctic seas.

	1	2	3	Vertical distribution (m)
<b>GASTROPODA PROSOBRANCHIA</b>				
Scissurellidae				
<i>Scissurella crispata</i> Fleming	×	×	×	1) 8–2000. 2,3) 2500–2700 to 2900–3000
Skeneidae				
<i>Anekes undulisculpta</i> Bouchet & Warén		×		2470 to 3213
<i>Ganesa bujnitzkii</i> Gorbunov			×	3800
<i>Lissospira profunda</i> Friele		×		2930–3800
<i>L. turgida</i> (Odhner)		×		2700 to 3350–3670
Rissoidae				
<i>Cingula griegi</i> (Friele)		×		2438
<i>Pseudosetia semipellucida</i> (Friele)		×		2470–3200
Eulimidae				
<i>Crinolamia dahli</i> Bouchet & Warén		×		2470–3709
Trichotropidae				
<i>Torellia vestita</i> Jeffreys	×	×	×	1) bathyal, upper abyssal; 2, 3) 200 to 3350–3670
Naticidae				
<i>Natica bathybii</i> Friele		×	×	150—about 3000
Incerta sedis				
Mesogastropod sp.n. Bouchet & Warén		×		2500–2700 to 3200
Buccinidae				
<i>Tacita danielsseni</i> (Friele)		×	×	(?1500) 2000 to 3709
<i>Mohnia mohni</i> (Friele)		×	×	1098 to 2250–3670
Turridae				
<i>Oenopota ovalis</i> (Friele)	×	×		1) bathyal, abyssal; 2) (557) 932 to 2500–2700
<i>Pleurotomella packardi</i> Verrill	×	×		1) bathyal; 2) (750) to 3000–3200
<b>GASTROPODA OPISTHOBRANCHIA</b>				
Scaphandridae				
<i>Cylichna lemchei</i> Bouchet & Warén		×		2500–2700
<i>Cylichnium africanum</i> (Locard)	×	×		1) 1400 to 2150; 2) 3000 to 3350–3670
Diaphanidae				
<i>Diaphana lactea</i> (Jeffreys)		×	×	1) abyssal; 2) 1300 to 3200
<b>SCAPHOPODA</b>				
Siphonodentaliidae				
<i>Siphonodentalium laubieri</i> Bouchet & Warén		×	×	2277 to 2500
<b>BIVALVIA</b>				
Nuculidae				
<i>Nucula zophos</i> Clarke			×	530 to 2277
Nuculanidae				
<i>Tindaria derjugini</i> Gorbunov		×	×	(1180) to 2500
<i>Portlandia arctica</i> (Gray)		×	×	10 to 2560
<i>P. frigida</i> (Torell)		×	×	8–9 to 2560
<i>Katadesmia kolthoffi</i> (Hägg)		×	×	2400 to 3800
<i>Yoldiella annenkovae</i> Gorbunov		×	×	698 to (2460)
<i>Y. frami</i> n.sp.			×	(2300) to (3965)
<i>Y. intermedia</i> (M. Sars)		×	×	11–17 to 3800
<i>Ledella tamara</i> Gorbunov			×	(530) 584 to 2212 (3800)



Arcidae			
<i>Bathyarca frielei</i> Jeffreys	×	×	18 to 3670
Mytilidae			
<i>Dacrydium ? vitreum</i> (Møller)	×	×	to 1800
Pectinidae			
<i>Similipecten greenlandicus</i> (Sowerby)	×	×	5 to 2000
<i>Hyalopecten frigidus</i> (Jensen)	×	×	1090 to 3350–3670
Montacutidae			
<i>Axinodon symmetros</i> (Jeffreys)	×	×	1) abyssal; 2) 2500 to 3210
<i>Axinodon</i> sp.	×	×	2500 to 3350–3670
Verticordiidae			
<i>Policordia jeffreysi</i> (Friele)	×	×	1666 to 3709
Cuspidariidae			
<i>Cuspidaria centobi</i> Bouchet & Warén	×	×	2500 to 3709
<i>Cuspidaria</i> sp.		×	(2300)
Total number: 1: 8; 2: 31; 3: 22.			

1: Adjacent part of the Atlantic Ocean. 2: Norwegian Sea. 3: Arctic Ocean. Depths of shells or valves are in ().

*Comments on some of the species listed in table 1.*

*Scissurella crispata* and *Torellia vestita*. Bouchet & Warén (1979) do not consider these true abyssal species.

*Portlandia arctica*. Essentially a littoral species known from depths less than 400 m; Bernard recorded lived specimens from 2560 m.

*Yoldiella intermedia*. A littoral species, most records from 50 to 500–600 m. Gorbunov (1946b) listed the species from a depth of 3800 m; this record should be confirmed.

*Similipecten greenlandicus*. This is mainly a littoral species with most records from 60 to 70 m; Hägg (1904) and Gorbunov (1946b) recorded it living at depths of about 2000 m.

All the above species should be considered 'guests' from the overlying zones; the species are occasionally able to establish themselves in the abyssal zone.

*Dacrydium vitreum* (Møller). Jensen (1912, p. 54) assigned a specimen from 1900 m depth, south of Jan Mayen, to *D. vitreum*; if the assignment is correct, it constitutes another 'guest' species; if not it may be another endemic abyssal species. Jensen also recorded *D. vitreum* from 2258 m, Davis Strait.

*Bathyarca frielei* has an extensive vertical distribution: there are numerous abyssal records, some bathyal and a few littoral records; the species may be considered an abyssal one that in some regions (such as East Greenland) is able to ascend into the bathyal zone and even into the littoral zone.

In all, 36 taxa of molluscs are presently known from the Arctic abyssal zone. The knowledge is based on the results of only 80 dredging stations, and thus is far from complete. The table shows that among the Opisthobranchia, only the order Bullomorpha is represented. It is seen that 6 gastropods and 1 (2) bivalves also occur in the North Atlantic. Some of these should be considered as 'guests' in the arctic abyssal zone, and occur permanently in the littoral and/or bathyal zone of the Norwegian Sea: *Pleurotomella packardi*, *Cylichnium africanum*, *Diaphana lactea*. A total of 31 species are known from the Norwegian Sea, whereas only 22 species have been recorded in the Arctic Ocean; 6 of the latter species have not yet been recorded from the Norwegian Sea, whereas the Norwegian Sea has 11 species not known from the Arctic Ocean; The difference is undoubtedly due to lack of sufficient investigation.

It is hardly possible from Table 1 to draw any conclusion as to the upper limitation of the abyssal zone. It is, however, possible to point out some species for which there are a

sufficient number of records (10–50) that the species may safely be considered as endemic abyssal species:

*Tacita danielsseni*, *Mohnia mohni*, *Katadesmia kolthoffi*, *Hyalopecten frigidus*, *Policordia jeffreysi*, *Cuspidaria centobi*.

The species listed have been recorded both in the Norwegian Sea and the Arctic Ocean and their upper limit varies between about 1100 and 2500 m.

*Bathyarca frielei* has an extraordinarily wide vertical range: Ockelmann (1958) mentions a live specimen from a depth of 18–21 m off East Greenland and several records between 250 and 780 m.

Thus the Arctic abyssal mollusc fauna appears to be composed of the following elements: 1) endemic abyssal species; 2) species having their main distribution in the bathyal zone and occurring as 'guest' species in the abyssal zone; 3) species from the North Atlantic; and 4) species ranging from the littoral to the abyssal zone.

#### *Mode of life of some bivalves*

Stanley (1970, 1972) studied the mode of life of Recent littoral bivalves with the purpose of applying the results on extinct taxa. He coined the terms 'endobyssate', i.e., forms byssally attached, but living partly or entirely buried into soft sediment, and 'epibyssate', i.e., forms byssally attached as epifauna fixed to a hard substratum. Stanley concluded that one of the most important ecological requirements influencing bivalve behaviour and adaptive morphology is the maintenance of physical stability. The ability to borrow rapidly is important for bivalves living in mud. Knudsen (1979) attempted to apply Stanley's results to deep-sea molluscs of the world ocean, concluding that they represented a wide diversity in the mode of life and reflected a multitude of ecological niches in the abyssal zone. In the following, the mode of life of some abyssal bivalves from the Arctic will be considered:

*Bathyarca frielei*: Stanley (1970) investigated a number of species of Arcidae and found that shell shape as expressed by the Length/Height (L/H) ratio reflected different modes of life; thus a ratio  $>1.35$  indicates an epibyssate species, while a lower ratio points to an endobyssate mode of life. In *B. frielei* the L/H ratio varies between 1.10 and 1.30, and an examination of specimens with soft parts disclosed the presence of a single fine byssus thread. Thus the species is an endobyssate form.

*Dacrydium*: Most (or all?) species have a byssus, build nests and are endobyssate (Knudsen 1979, Ockelmann 1983).

*Hyalopecten frigidus*: Examination of alcohol specimens with soft parts showed that in most a byssus could be observed; it consists of a stout short thread, distally split up; the specimens lacking a byssus could have lost it during capture or preservation. Stanley (1970) studied the swimming ability of pectinids of various shapes. He found that in free-living species the shell is broad in a direction parallel to the hinge axis and the auricles are rather symmetrical. The presence of a byssus, the shape of the valve and the asymmetrical auricles point toward a byssate mode of life and a poorly developed ability to swim in *H. frigidus*.

*Policordia jeffreysi*: Allen & Turner (1974) observed that some species of *Lyonsiella* had particles of sediment and remains of spicules, foraminiferan tests, etc. adhering to the shell. They also observed radial mantle glands supposed to have an adhesive function, and fine byssus threads were seen in several species. Prezant (1979a, b) studying *Lyonsia hyalina*, observed that small conical projections on the periostracum covering the outer surface helped to entangle a mucoid secretion produced by the radial mantle glands. The mucus affixes sand grains to the shell. It is suggested that the sand cover stabilizes the bivalve in

the substratum and lends some protection to the thin shell. Morton (1981) observed the same phenomenon in *Periploma angasai* and summarized earlier observations. Bouchet & Warén (1979) did not find any byssus in their specimens, although a byssus gland was observed. In the present material, the smaller specimens (about 13 mm long) have a well-developed byssus consisting of numerous threads which are split distally and have particles affixed to the distal ends. The two largest specimens did not have any byssus. One of them, about 20 mm long ('Lynch'), had a solid coating of soft bottom sediment, leaving only the umbonal part exposed. Thus it appears that smaller specimens of *P. jeffreysi* anchor themselves by a byssus, while larger ones rely on a coating for stabilization. The other large specimen, about 25 mm long ('Ingolf' St. 113) had neither byssus nor coating; it remains unknown whether it originally had a coating which was rubbed off or lost during the capture and subsequent handling. The smaller specimens referred to were all devoid of any trace of coating.

*Reproduction:* Bouchet & Warén (1979) measured the larval shells of nearly all the 24 species of gastropods and bivalves they dealt with and studied the egg capsules of 5 species of gastropods, which all were found to have a direct development. Another 5 species had pelagic development and all occurred south of the North Atlantic Ridge. The remaining 14 species had direct or lecithotrophic development. In the present survey this type of larval development was found in 2 additional species *Nucula zophos* and *Yoldia frami*, having prodissoconchs of 350 and 300  $\mu\text{m}$  respectively.

*Feeding:* Bouchet & Warén (1979) examined the stomach contents in most of their species but identification of the contents was possible only in 5 species. They observed that the stomach of species of Skeneidae contained detritus and foraminiferans, and that *Crinolamia* (Eulimidae) probably parasitises a crinoid; *Tacita* (Buccinidae) contained polychaete and sponge remains and the unknown mesogastropod remains of sponges. In addition *Natica* (Naticidae) and *Mohnia* (Buccinidae) are predators. In *Cylichnium* (Scaphandridae) several foraminiferans were found in the stomach.

Bouchet & Warén (1979) noted that *Axinodon symmetros* (Montacutidae) lives associated with the spatangoid urchin *Pourtalesia jeffreysi* Wyville Thomson, suggesting that it feeds on suspended bacteria; they did not make any comments on the remaining bivalves.

The Nuculidae and the Nuculanidae are primarily deposit feeders. *Bathyarca frielei* is a suspension feeder. Morton (1982) studied its close relative *B. pectunculoides*, a bathyal species from the North Atlantic and the Norwegian Sea. He found a spectacular posterior extension of the mantle serving as a simple siphon. I have seen a similar formation in *B. frielei*; it may be concluded that the species is a suspension feeder, as is also *Hyalopecten frigidus*. *Policordia* and *Cuspidaria* belong to families in which all members are predators, living on small crustaceans (copepods, isopods, amphipods).

From the remarks on the mode life and feeding it can be concluded that the Arctic abyssal region presents a considerable ecological diversity. It is noteworthy that two suspension feeders, *B. frielei* and *H. frigidus*, are among the largest species present with the exception of *Policordia* and, judging from the number of records and number of specimens obtained, also among the most abundant forms.

#### ACKNOWLEDGEMENTS

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# NEW TAXA OF *GULELLA* L. PFR. AND *PTYCHOTREMA* MÖRCH (MOLLUSCA, STREPTAXIDAE) FROM EASTERN AFRICA

BERNARD VERDCOURT<sup>1</sup>

(Accepted for publication, 18 May 1985)

*Abstract*: One new subgenus and 7 new species of *Gulella* and a new subspecies of *Ptychotrema tschibindanum* are described from the collection made by Åke Holm in East Africa and Ethiopia whilst on spider-collecting expeditions. Some comments are also made on already described but poorly known species.

## INTRODUCTION

Åke Holm collected spiders in East Africa over a period of 45 years for the Natural History Museum in Stockholm and naturally came across many molluscs while so doing; these he also collected assiduously but unfortunately all were placed in spirit mostly of a slightly acid nature and as a result many shells are in rather poor condition. Since the collection is undoubtedly one of the major contributions to the study of East African Mollusca it is particularly unfortunate that the preservation is unsatisfactory. It is important, however, that as much information as possible is obtained from this material and it is proposed to publish this in a series of papers of which this is the first. The whole material was kindly loaned to me by Dr. Åke Anderson of the Natural History Museum, Stockholm consisting of some hundreds of specimens. I have identified this material as completely as possible and a book of identifications and notes has been compiled to accompany the collection. This first contribution deals with the more interesting Streptaxidae.

## SYSTEMATICS FAMILY STREPTAXIDAE

### **Gulella** L. Pfeiffer

Subgenus **Sphincterocochlion** subg. nov.

*Description*: Shell small, tapering cylindrical, the whorls smooth and glossy save for very fine incised spiral lines. Aperture much constricted; parietal process occupying all of the parietal wall with 2 lobes but no angular lamella; outer lip characteristically infolded and with 2-lobed shelf.

*Etymology*: Derived from σφιγκτήρ that which binds tight and κοχλίων a small mollusc with a spiral shell. If raised to generic rank it will be of neuter gender.

*Type species*: *Gulella sphincterocochlion* sp. nov.

*Additional Species*: None

*Remarks*: Continued work on the Holm collection has revealed a number of new species including a very remarkable streptaxid from just below the alpine zone of the Ruwenzori Range. I have referred it to a separate subgenus of *Gulella* but am well aware it is unlike any

<sup>1</sup> Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB.



previously described species. Without a great deal of further anatomical information the classification of all the elements referred to this protean genus is impossible and I have preferred not to erect a new genus at this stage.

**Gulella sphincterocochlion** sp. nov. Fig. 1.

*Description:* Shell small, tapering subcylindrical, imperforate, glossy, creamy white but doubtless more or less transparent in fresh state; spire elongate, the sides slightly convex, the apex broadly rounded. Whorls 7, increasing irregularly, the second visible whorl longer than either the third or fourth, the body-whorl as long as the four above it, slightly convex, appearing smooth but with very fine incised spiral striae about 25–50  $\mu\text{m}$  apart, scarcely visible under a  $\times 10$  hand-lens and also very occasional transverse arrested growth-stage lines; suture simple, not deeply incised. Aperture severely constricted, roughly L-shaped the actual mouth consisting of 4 interconnected widenings or sinuses and 4 basic processes; parietal wall with two relatively large rounded processes, the lower slightly the larger but with no true angular lamella; outer lip with a large central convex infolding which when viewed laterally is seen as two equal rounded emarginations, the junction of which appears as a median projection of the peristome; columella convex but with a shallow concavity when viewed in plan causing the columella edge to be margined and with a rounded process beneath it but no truly basa process. Animal unknown.

*Dimensions:* Height 4.2 mm, breadth 1.4 mm, length of body-whorl 2 mm, height of aperture 1.2 mm, breadth 1.1 mm.

*Distribution:* Uganda, Ruwenzori, Bujuku Valley, Kyanasabu Camp, by sifting moss, 2850 m, 19 Mar. 1948, Åke Holm 28 (holotype in Natural History Museum, Stockholm). No other material seen.

Section **Silvigulella** Pilsbry, 1919.

*Remarks:* Pilsbry erected this new section for a slender species described from a single specimen found in the Rutshuru gallery forest in E. Zaire. He suggested that *G. filicosta* (Morelet) described from Angola belonged to the same group. Connolly later described *G. pisa* from N. Kenya and there is also a further undescribed species left under a manuscript name *Streptostele ariel* by Preston. M. Pickford of the National Museum, Nairobi has recently discovered numerous specimens of *G. pisa* (formerly known only from the type) at Kora on the Tana R. (see Verdcourt 1982, 4 adnot.). I have a note made many years ago that the British Museum specimen of this bears the very vague locality Mbarara to Kigezi and a note by Connolly synonymising it with *G. osborni*. A re-examination of the specimen confirms this although there are certain minor differences in the dentition. Another species has been detected in the present collection unfortunately also represented only by a slightly damaged singleton. It is, however, so distinctive that I have not hesitated to describe it. It differs from *G. pisa*, its closest ally, in having more than a simple inset upper lobe on the columella; *G. filicosta* is quite different in possessing a bifid mid-columella lobe and a median indentation on the outer lip. *G. osborni* Pilsbry has a less tapering shorter shell with one less visible whorl and differently disposed columella folds, one of which is on the peristome. *Silvigulella* is probably not a natural grouping.

**Gulella lacus-paradisiaci** sp. nov. Fig. 2.

*Description:* Shell small, tapering subcylindrical, (perforation obscured) probably glossy when fresh and translucent white; spire elongate, the sides very slightly convex, practically straight in the upper part, the apex rather narrowly rounded. Whorls  $7\frac{1}{2}$ , increasing more or less regularly, slightly convex with median parts almost straight and in fact the body-whorl when viewed from the back at a certain angle can be seen to have a median concave area near the peristome more or less corresponding to the outer lip lobe; apex worn but at

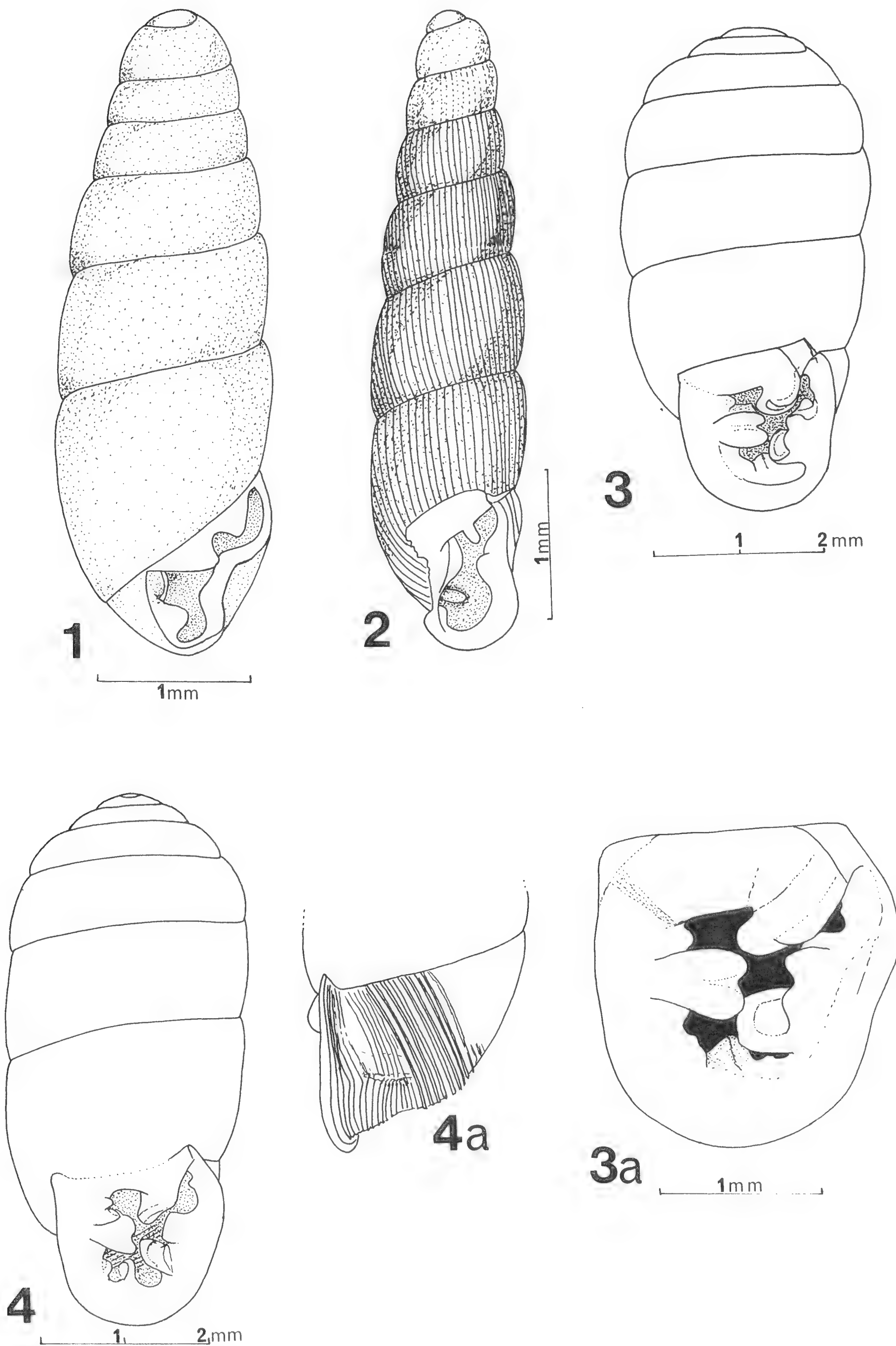


Fig. 1. *Gulella sphincterocochlion* sp. nov. Uganda, Ruwenzori. Shell.  
 Fig. 2. *Gulella lacus-paradisiaci* sp. nov. Kenya, Marsabit. Shell.  
 Figs. 3,3a. *Gulella aekei* sp. nov. Kenya, Mathews Range. Shell.  
 Figs. 4,4a. *Gulella aversostriata* sp. nov. Kenya, Mt. Elgon. Shell.

least initial two whorls probably smooth but the rest very strongly ribbed, about 22 visible from above on body whorl and 28 on the one above; suture serrated by the ribs but obscured, not deeply incised. Aperture slightly damaged, elongate-quadrate; a more or less centrally placed slightly curved parietal lamella; a massive trianguloid process on the outer lip with middle of upper edge shallowly indented which with the parietal lamella cuts off the upper left hand sinus; an upwardly directed sinuous columella fold with a small nodule at the base of the columella and a transversely elliptic pustule at the back of the aperture far within the outer lip placed so that it is visible in the sinus between the columella fold and the basal columella nodule; the peristome is broadly flanged, probably all round but broken in the available specimen.

*Dimensions:* Height 4.3 mm, breadth 1 mm, height of aperture 1 mm, breadth 0.75 mm.

*Distribution:* Kenya, Mt. Marsabit, Lake Paradise, crater rim, 1400 m, 1 Feb. 1969, Åke Holm 152 (holotype in the Natural History Museum, Stockholm).

Section **Molarella** Connolly, 1922.

**Gulella aekei** sp. nov. Figs. 3, 3a.

*Description:* Shell oblong but widest towards the apex and slightly but distinctly tapering towards the aperture, narrowly perforate, the whorls smooth and glossy save at the base, creamy white; spire well-developed, the sides slightly convex, the apex broadly dome-shaped. Whorls 7, regularly increasing, slightly convex, smooth save for irregular growth-lines a few of which are somewhat rib-like; on the last whorl, however, behind the peristome and extending right around the umbilicus are strong transverse ribs spaced at about 12 per mm with a fairly strong spiral element which does not cut the ribs; only the ribs immediately behind the peristome extend upwards to the suture which is simple and lightly impressed. Aperture square with rounded base; peristome thickened and flanged and dentition complicated; angular parietal lamella running inwards and deeply excavated on the right-hand side and within with another flange at right angles; the sinus to the right hand side of this parietal process bears at the top left hand side a small nodule with a faint convexity beneath it; outer lip process grooved at right angles to plane of aperture, the groove running inwards and across the top in the plane of the aperture so that it appears broadly bifid and at the base developed into a conspicuous lobe which partially obscure a deeply inset transverse basal lobe; the columella bears a conspicuous bifid process distinctly narrowed where its shank meets the peristome; this process continues back into the aperture as a broad lobe; above this process is a small nodule and below it a curved fold just obscuring the right hand side of the basal lobe.

*Dimensions:* Height 5.7 mm, breadth 2.9 mm, height of aperture 2.1 mm, breadth 1.9 mm.

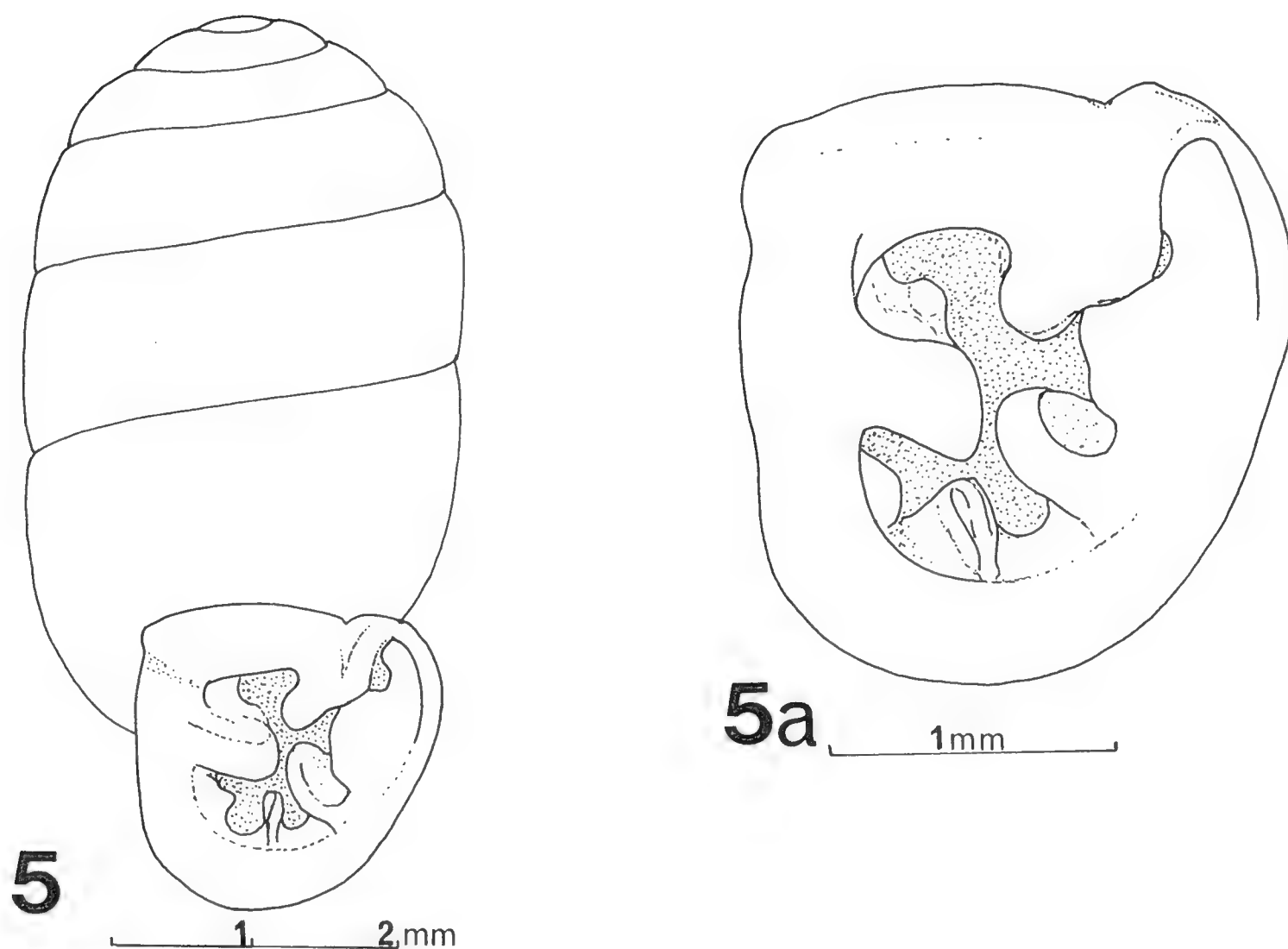
*Distribution:* Kenya, Mathews Range, warges (= urgues, Uaraguess, etc.), in litter of *Podocarpus* forest, 1750 m, with juvenile *Krapfiella princeps* Preston and *Gulella* cf. *pretiosa* (Preston), Åke Holm 335 (holotype in the Natural History Museum, Stockholm).

*Remarks:* The curious narrowing of the bifid columella process and complicated lobing of the parietal and outer lip processes clearly distinguish this from any other species in the section. The Mathews Range peaks, isolated for many thousands of years, are well-known for their endemic molluscs so this addition is not surprising.

**Gulella aversostriata** sp. nov. Figs. 4, 4a.

*Description:* Shell oblong-cylindrical, very slightly tapering towards the base, imperforate but with a deep marginally grooved depressed area corresponding to the columellar process, creamy white; spire elongate, the sides more or less straight, the apex broadly dome-shaped. Whorls 7, increasing regularly, body and early ones slightly convex but the two middle ones almost flat, smooth and shining save for scattered growth-lines and some very faint close spiral scratches but on the body whorl behind the peristome there is a series





Figs. 5,5a. *Gulella aversostriata* sp. nov. var. Kenya, Mt. Elgon. Shell.

of about 20 strong ribs which are fainter and angular before and within the pit corresponding to the labral process and much stronger and straighter beyond it; beyond these are a further 10 ribs surrounding the umbilical area but not crossing even half the height of the whorl; between the outer ribs are a series of small very shallow pits; suture simple slightly impressed. Aperture squarish with rounded base the dentition complicated; angular lamella strong, rather sinuous and excavated on the right hand side; the labral process consists of two parts born on the part of the outer wall corresponding to the outer pit and sufficiently separate with part of the wall visible between for the two parts to be designated separate lamellae; within the sinus cut off by the parietal and labral processes there is a small nodule on the outer lip; a distinct basal lamella; a central bifid process on the columella with a nodule both above and beneath it.

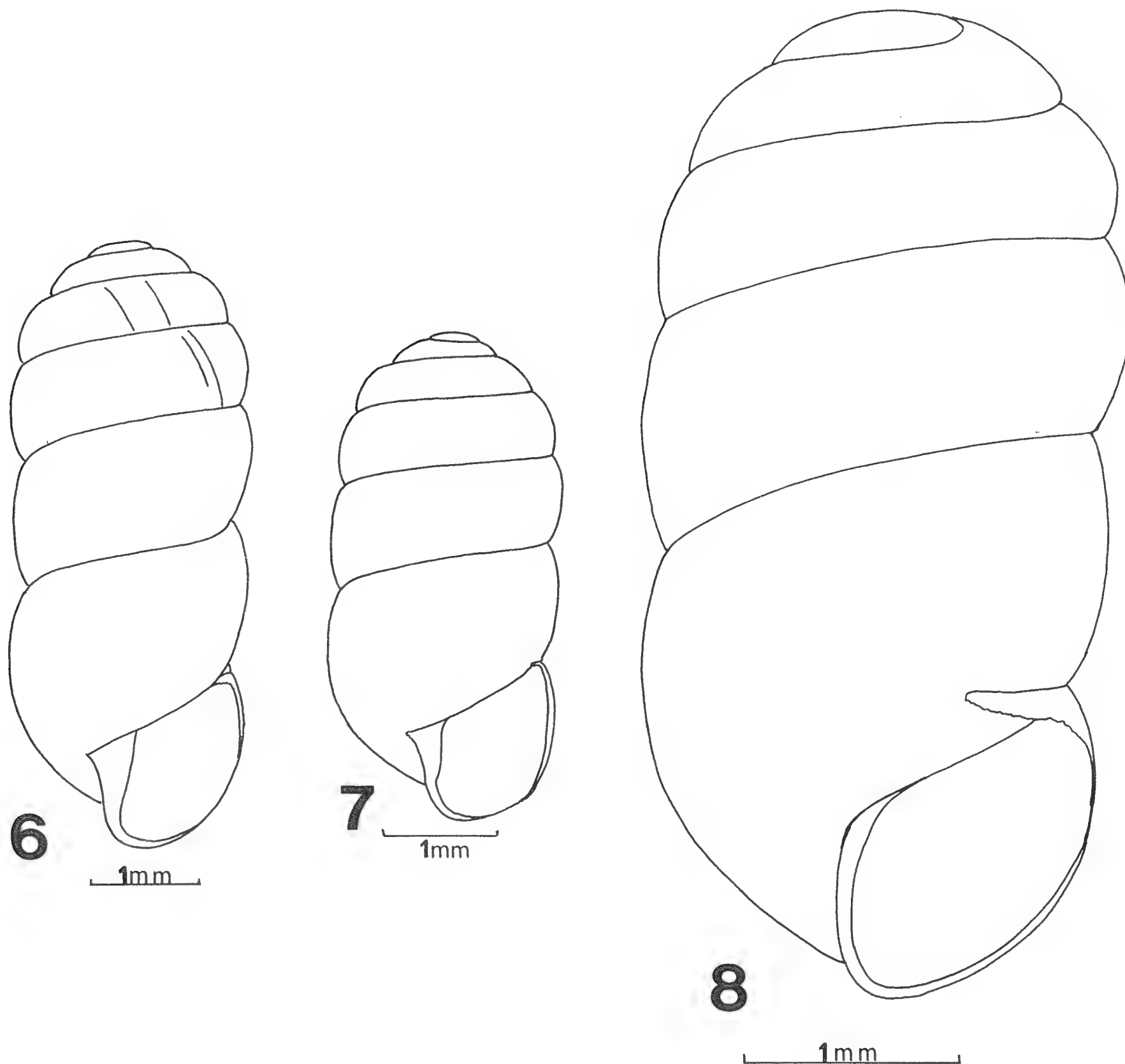
*Dimensions:* Height 6.25 mm, breadth 2.8 mm, height of aperture 2.1 mm, width 1.9 mm.

*Distribution:* Kenya, Mt. Elgon, Kaptega R., litter in gallery forest, 1900 m, 11 Dec. 1977, Åke Holm 383 (holotype in the Natural History Museum Stockholm).

*Remarks:* It is well-known that there is a good deal of variation in the apertural dentition in *Gulella* which is easy to assess when series of specimens are available. About 10 years earlier Dr. Holm had collected another single specimen of a *Gulella* in the same locality which I am convinced is conspecific although it differs in the columella process not being bifid, the absence of the small nodule above the process and a slightly wider contour (6.5×3.5 mm). I have figured this specimen for comparison but do not designate it a paratype. (Figs. 5,5a).

*Distribution:* Kenya, Mt. Elgon, Kaptega R., 1920 m, 12 Jan 1966, Åke Holm 66 (Natural History Museum, Stockholm).

It is clear that *G. aekei* and *G. aversostriata* are very closely related but there are some fundamental differences in dentition.



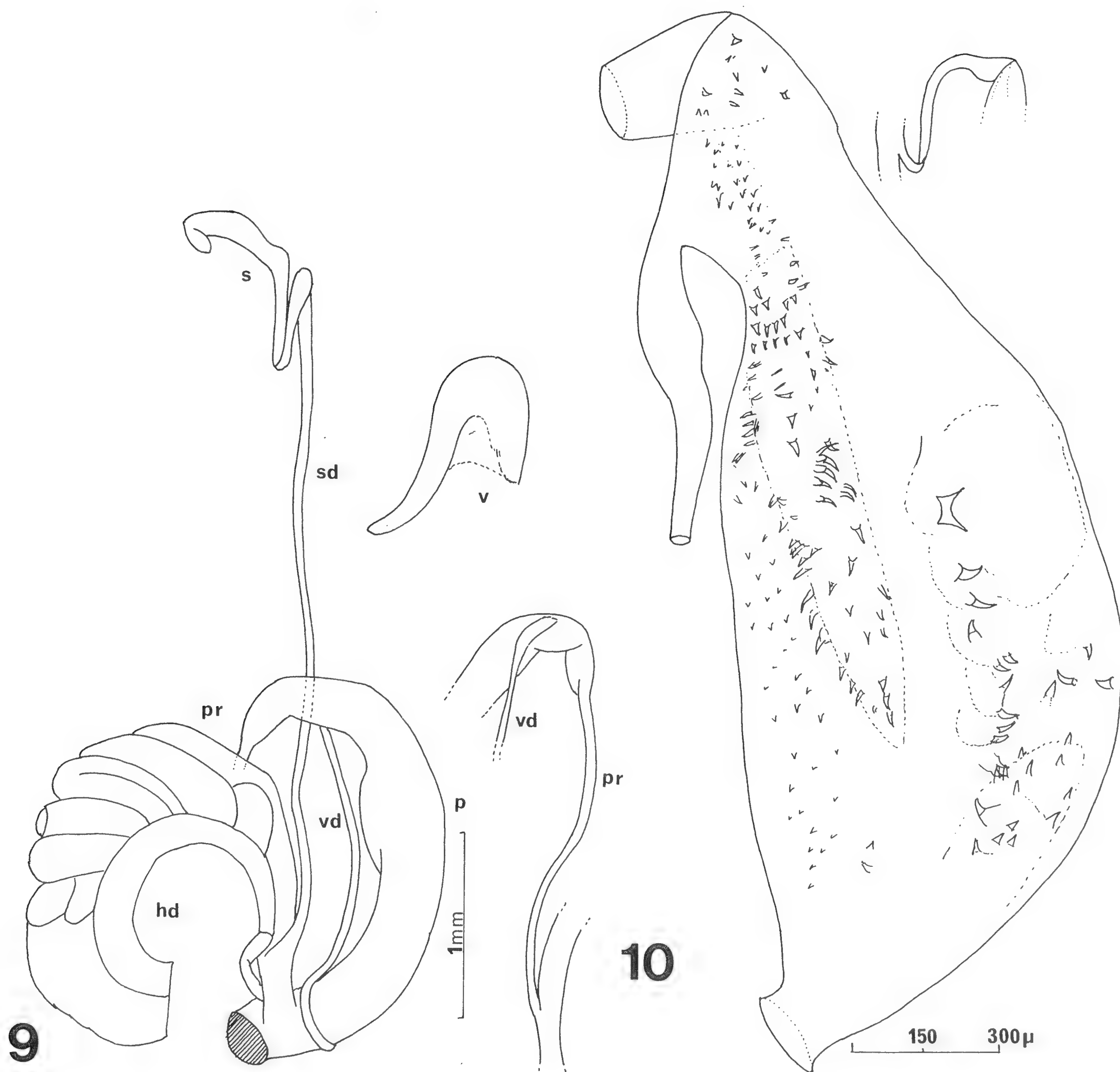
Figs. 6–10. *Gulella ngorongoroensis* sp. nov. 5, 7, 8 Shells. 9 part of genitalia. 10 penis opened to show armature.

Section: **with no apertural dentition**

*Remarks:* A number of species has been described with no apertural dentition (see Verdcourt 1962, p. 5) and even the generic classification of these is unsatisfactory. It is certain that the genital anatomy, particularly the armature of the penis will help to clarify matters. It is therefore valuable to obtain from the Holm collection what information there is.

***Gulella ngorongoroensis* sp. nov.** Figs. 6–10.

*Description:* Shell variable, oblong to elongate-oblong, mostly very slightly widened towards the apex, with narrow umbilicus (which might be closed over by the columella in more perfect shells, greyish olive-white but probably white or green in life and probably glossy; spire produced, the sides more or less straight, the apex very obtusely rounded. Whorls 6, moderately convex, gradually increasing; apex more or less smooth and the rest also smooth save for irregular coarse growth lines but no regular striation; faint traces of spiral scratches; suture well-marked, not crenulate but irregular due to growth lines. Aperture oblong-elliptic or obliquely narrowly ovate with no dentition; peristome thickened in the columella area.



*Dimensions of holotype:* height 5.6 mm, breadth 2.2 mm, aperture 1.7 mm, length of last whorl 2.7 mm; *paratypes:* height 4.3–4.6 mm, breadth 2.1–2.3 mm, aperture 1.4 mm, last whorl 2.3 mm.

*Distribution:* Tanzania, Ngorongoro Crater Rim, 2250 m, 19 Mar. 1969, Å. Holm 223 & 224 (holotype and paratypes in Natural History Museum, Stockholm).

The preserved body is yellow, the mantle speckled with green and the ocular retractors green. The genital anatomy is partly shown in Fig. 9. The penis contains two pilasters covered with yellow spinules of assorted sizes (Fig. 10). The radula is 2.08 mm long, 0.47 mm wide and has about 55 rows and 8 main teeth in each half row with a small triangular central tooth; the 3 outer ones are much smaller, 2, 3, 4 & 5 are roughly equal the 2nd and 3rd just slightly the largest. The spinule pattern is very different from the simplified one occurring in *Gulella io* Verdcourt (Verdcourt 1979) and from those figured by Lopez and



Rocandio (1955) but not so dissimilar from that of *Holm* 150 from Kenya, Marsabit, Lake Paradise crater rim, 1400 m, 1 Feb. 1969 which has been identified as *G. cf. ingloria* (Preston) and has a similar gross genital anatomy. The Holm specimens do not, however, have the crenellate suture of *ingloria* (Fig. 11, 12). The nearest relative of *G. ngorongoroensis* would seem to be *G. simplicima* (Preston) but that has microscopical apical striae and stronger transverse striae.

*Gulella puella* Connolly. Fig. 13.

1929 *Gulella puella* Connolly, p. 173, Pl. 5, Fig. 1.

*Distribution*: Kenya, Elburgon, litter of *Eucalyptus* 'forests', 14 Dec. 1977 Å. Holm 385 (Natural History Museum, Stockholm).

*Remarks*: This species was first described from Naivasha and has also been found at Turi.

***Gulella dolichos* sp. nov.** Fig. 14.

*Description*: Shell very small, cylindrical, imperforate but with an umbilical depression, creamy-translucent, glossy; spire elongate, the sides straight, the apex broadly rounded. Whorls  $8\frac{1}{4}$ , gradually increasing slightly convex, the embryonal whorls rather large in proportion to the rest of the shell; initial whorls more or less smooth, the rest with fairly regular growth lines but no regular sculpture save for about 6 ribs on the outer wall behind the peristome and with a feeble spiral element between them; suture slightly impressed, strongly crenellate particularly bordering the body-whorl but crenellations becoming weaker above and not present between the initial whorls. Aperture triangular-ovate, the peristome thickened in the columella area and thinned at the top of the outer lip but scarcely with a sinus; a single parietal angular tooth sinuously entering set close to the right hand side; no obvious fold on the columella.

*Dimensions*: Height 2.58 mm, breadth 0.89 mm, height of aperture 0.63 mm, breadth 0.68 mm.

*Distribution*: Kenya, Mt. Marsabit, Lake Paradise, crater rim, 1400 m, 1 Feb. 1969, Å. Holm 152 (Holotype in Natural History Museum, Stockholm).

*Remarks*: A single living specimen was found together with *Streptostele* sp., *Gulella* (*Silvigulella*) *lacus-paradisiaci* Verdcourt, *G. pretiosa nyiroensis* (Preston), *G. cf. laqueus* (Preston), *Thapsia* sp., *Kaliella barrakporensis* (Pfeiffer), *Guppya cf. quadrisculpta* (Connolly), *G. cf. rumrutiensis* (Preston), *Pseudopeas* sp., *Conulinus* sp., *Maizania hildebrandti kibonotoensis* (D'Ailly) and *Tropidophora* (*Otopoma*) *letourneuxi* (Bourguignat). It appears to be totally unrelated to any previously described species but is perhaps closest to *G. magnolia* Connolly described from the Victoria Falls but that is larger with fewer whorls and the aperture and body-whorl are differently shaped.

Fig. 11, 12. *Gulella cf. ingloria* (Preston). Kenya, Marsabit. Shells.

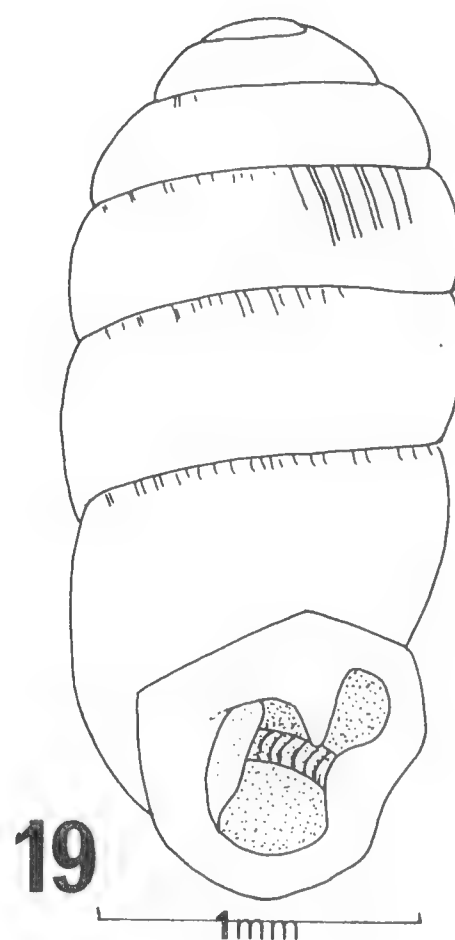
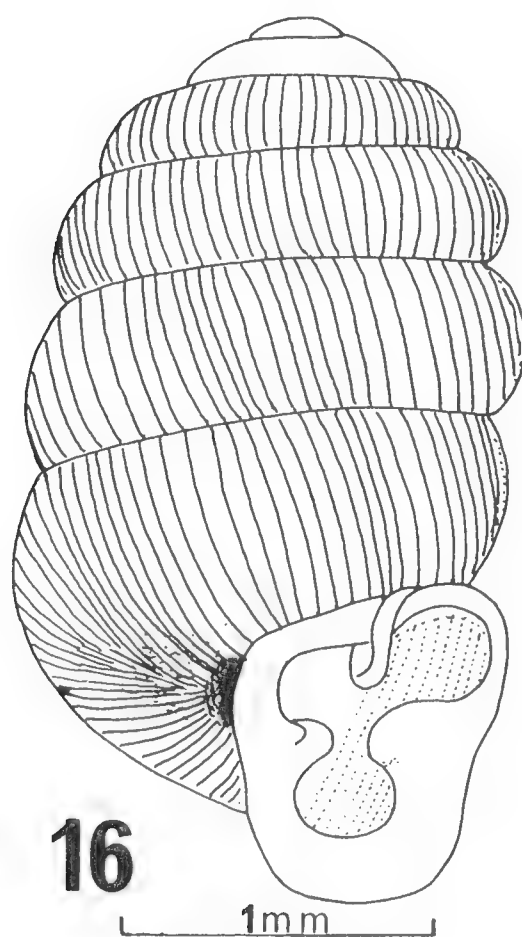
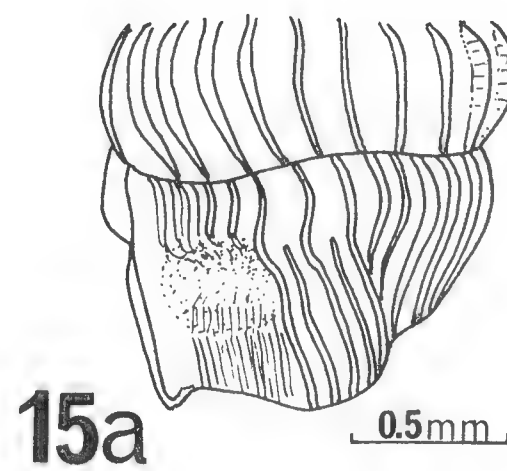
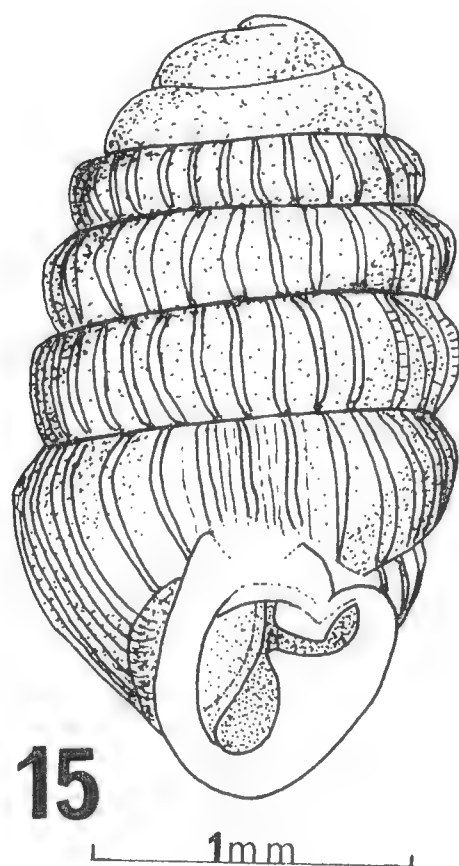
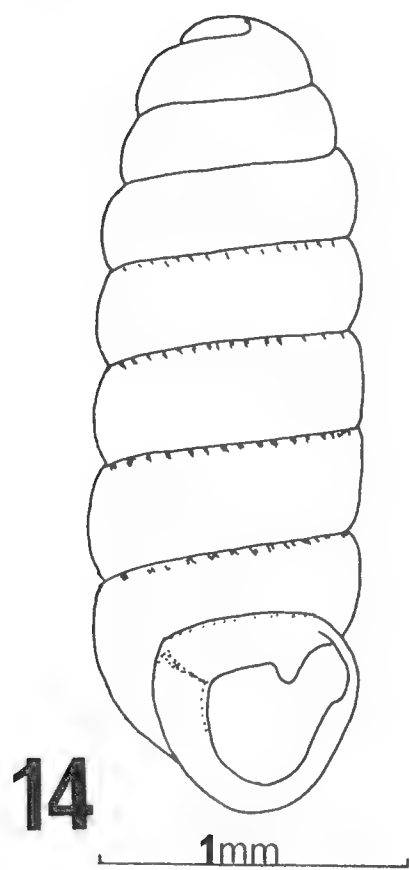
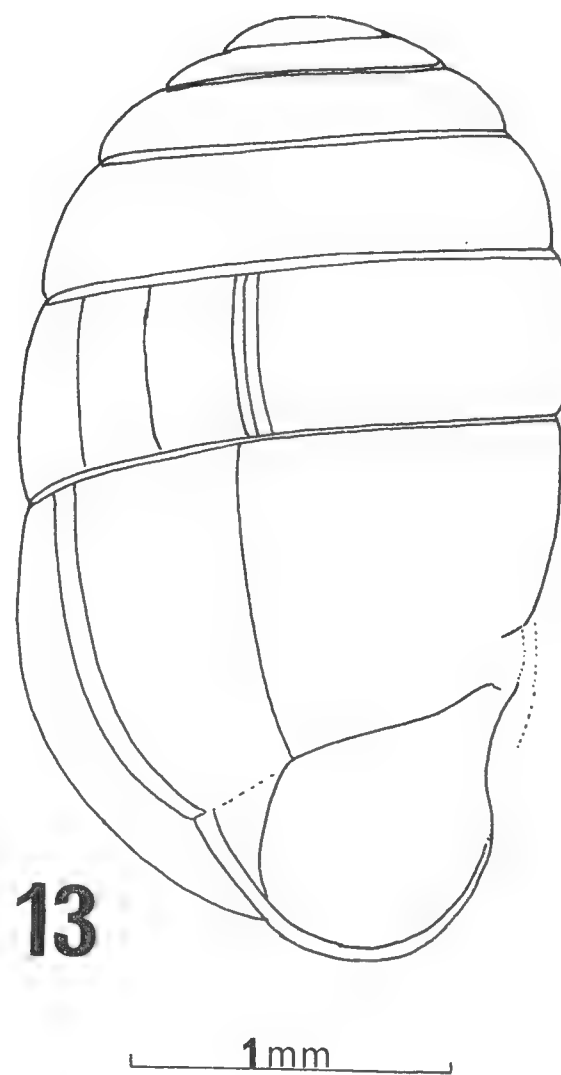
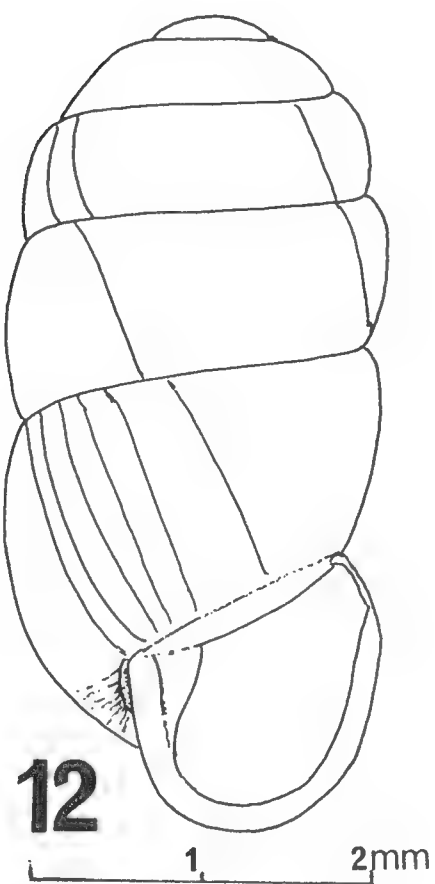
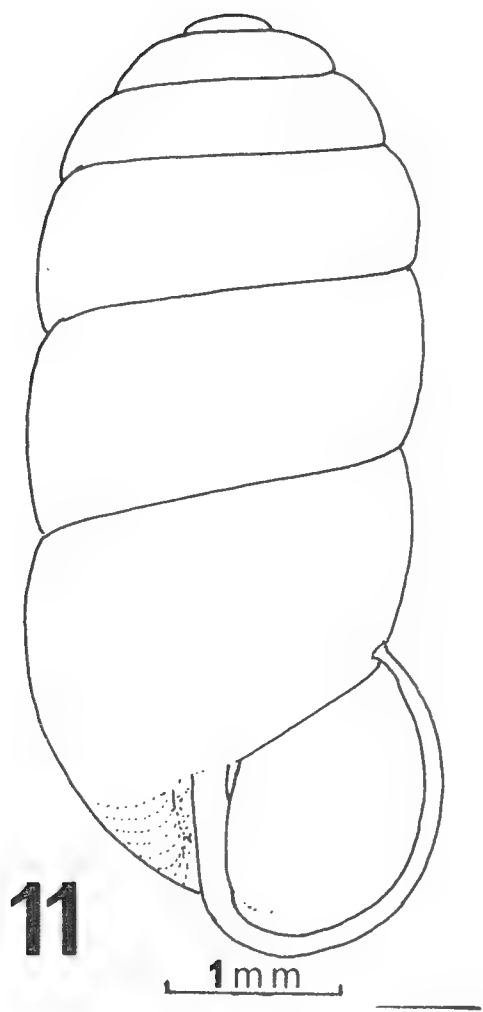
Fig. 13. *Gulella puella* Connolly. Kenya, Elburgon. Shell.

Fig. 14. *Gulella dolichos* sp. nov. Kenya, Mt. Marsabit. Shell.

Figs. 15, 15a. *Gulella filix* Connolly. Kenya, Cherangani Hills. Shell.

Fig. 16. *Gulella cf. princei* (Preston). Kenya, Mt. Elgon. Shell.

Fig. 19. *Ptychotrema tschibindandum septentrionale* ssp. nov. Ethiopia, 90 km. W. of Addis Ababa. Shell.



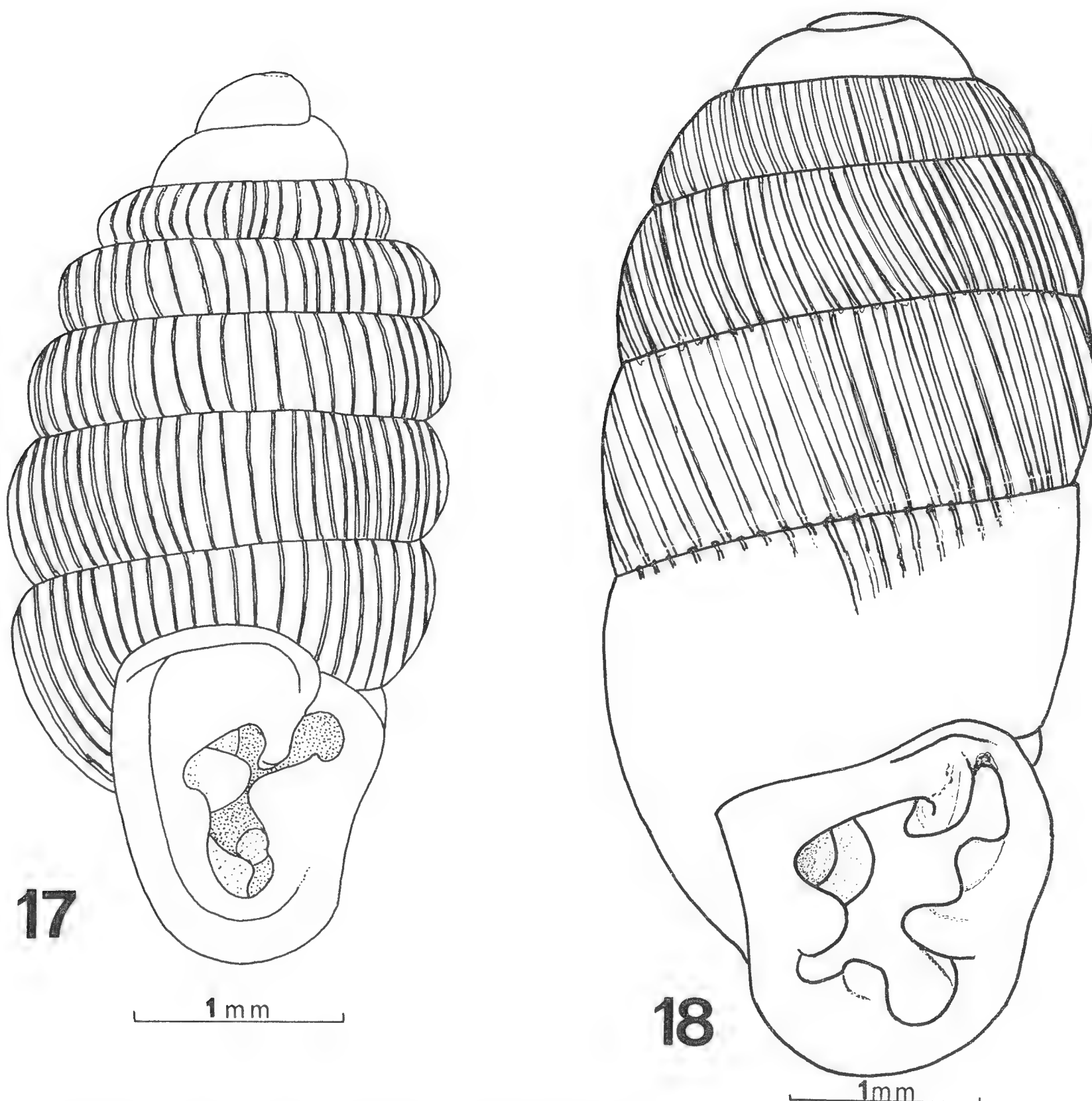


Fig. 17. *Gulella radius* (Preston). Kenya, 30 km. S. of Mombasa. Shell.

Figs. 18. *Gulella shoaensis* sp. nov. Ethiopia, 90 km. W. of Addis Ababa. Shell.

*Gulella filix* Connolly. Figs. 15, 15a

1922 *Gulella filix* Connolly 1922, p. 495, Pl. 14, Fig. 12.

*Description:* Shell very small, oblong-ellipsoid ('pupoid') with a slender lunate perforation, probably glossy in life, white; spire produced, the sides curved in outline, the apex bluntly rounded. Whorls 7, very convex, each widest above the middle, gradually increasing, the first whorl larger in proportion to the shell, the first  $2\frac{1}{2}$  more or less smooth, the rest with very strong narrow lamellae the four visibly lamellate whorls from base to apex bearing 13, 15, 14 and 15 lamellae in plan view respectively; lamellae somewhat angulate above the middle of the whorl and at least some with striae across their width; finer striation between the lamellae not visible in the specimen available save in one or two interstices immediately behind the aperture; suture well-marked. Aperture oblong, with only two teeth, a strong parietal tooth in the usual angular position and a large triangular process on the outer edge cutting off a sinus with the edge of the parietal tooth; columella and base with no external teeth but a deep margined lobe on the former. Peristome thick and well-developed; behind it and extending to the umbilical slit is a finely striate impressed subtriangular area and also the pit already mentioned followed by a laterally compressed bulge, the main ribs of



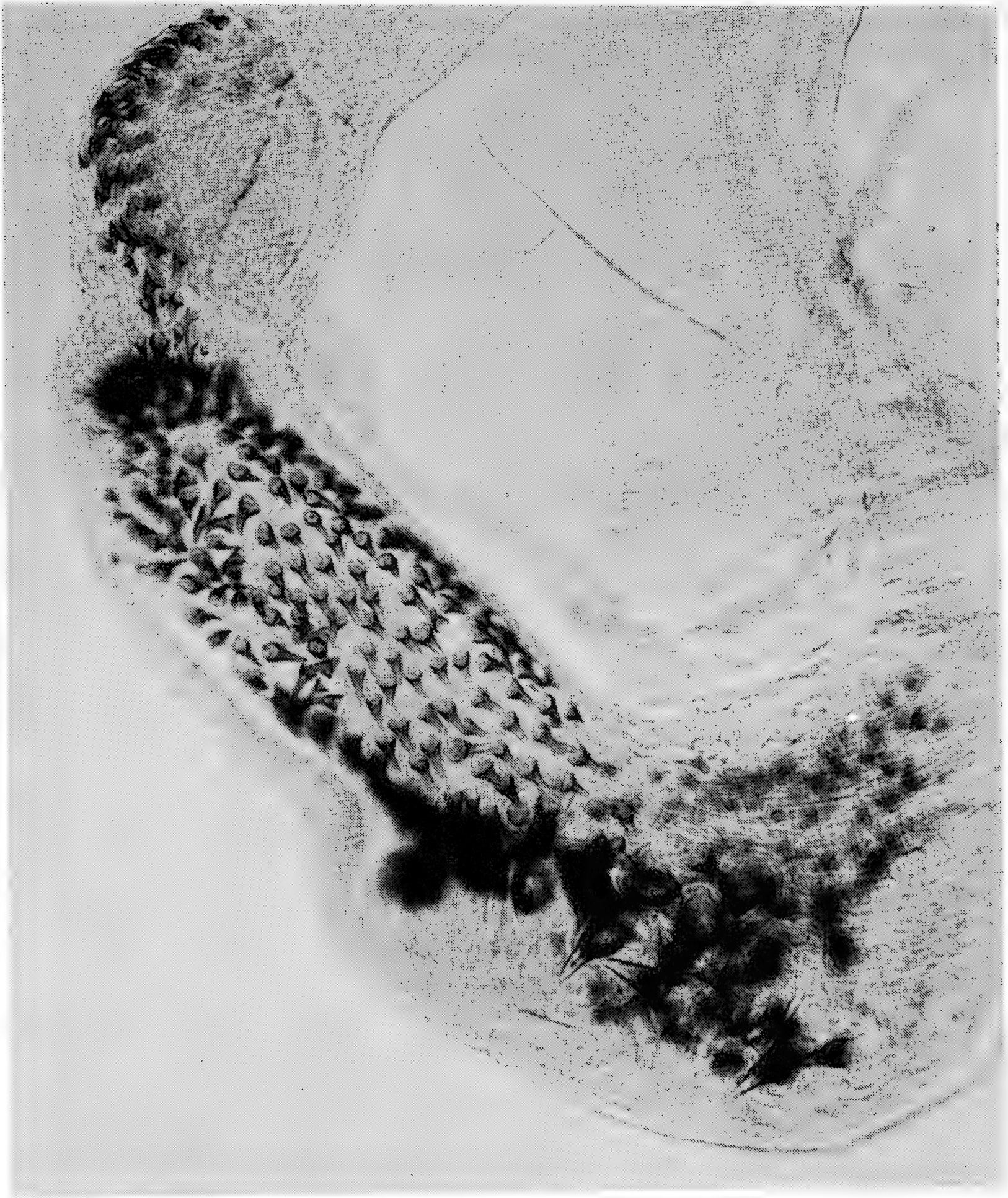


PLATE 12

*Gulella ingloria* (Preston). Kenya, Marsabit. Penis opened to show armature,  $\times 130$ .



which are strongly bent about 2/3 of the distance up the whorl but two intermediary ribs only extend as far as these bends; beyond this bulge the body whorl is flattened in the middle so as to appear roughly angled at top and bottom.

*Dimensions:* Height 2.5 mm, breadth 1.45 mm; height of aperture 0.8 mm, breadth 0.8 mm.

*Distribution:* Kenya, Uasin Gishu Plateau, Cedar Forest, 2550 m., Mrs Barber (holotype in Albany Museum, Grahamstown, paratype in British Museum (Nat. Hist.) 1937.12. 30. 530. 1); Cherangani Hills, Kapolet Forest, 1900 m, 7 Jan. 1965, Åke Holm 49 (Natural History Museum, Stockholm).

*Remarks:* This seems to be the only other recorded specimen of this species and I have prepared an improved description from it. Connolly's var *benetecta* is I think a distinct species.

*Gulella* cf. *princei* (Preston) Fig. 16.

1911 *Ennea princei* Preston, p. 466, Pl. 11, Fig. 7.

*Distribution:* Kenya, S. Mt. Elgon, Kimilili R., 2400 m, 30 Jan. 1965, Åke Holm 115 (Natural History Museum, Stockholm).

*Remarks:* A small shell 2.8×1.5 mm of 6¼ whorls, narrowly umbilicate; 1½ apical whorls appearing more or less smooth but with very fine spiral striae, some pits and some transverse element; rest of whorls with 23–28 striae per mm and a large pit behind the peristome. Aperture 1.1×0.8 mm. Much smaller than the types of *G. princei* and probably a new species; some species are, however, well known to vary greatly in size.

*Gulella radius* (Preston) Fig. 17.

1910 *Ennea radius* Preston, p. 529, Pl. 7, Fig. 8

1969 *Gulella radius* van Bruggen, p. 71.

*Distribution:* Kenya, 30 km S. of Mombasa, Diani Beach, 7 Mar. 1970, Åke Holm 249 (Natural History Museum, Stockholm).

*Remarks:* The rather few known specimens of *G. radius* exhibit a great deal of variation and it is not yet evident if there is a species aggregate or one very variable species. The latter seems more likely. The original description mentions a parietal tooth, a bifid outer lip process and a columella lobe. A shell<sup>1</sup> in the type collection (Kenya, Shimba Hills) of the British Museum (Nat. Hist.) has a small angular sinus between the main parietal and palatal teeth and three small broad folds, one on the columella and two at the base; the columella lobe is obscured. In the general collection is a shell from Tanzania, Dar es Salaam with a narrow rectangular main palatal slab with an upper tooth, two inset basal teeth and a rectantangular tooth midway up the columella side of the inner peristome. A specimen from Kenya, Gazi in the Laboratoire de Malacologie, Paris has a very distinct sinus with edges of the parietal tooth and palatal slab closely parallel, an inset right-hand basal tooth, small raised nodules at base and apex of the columella margin and an inset fold on the columella itself produced in the middle. Material from Kenya, Mrima Hill has the two lowermost teeth small and very inset, the upper columella process a mere thickening of the columella margin and the columella lobe with a prominent rounded process in its middle. Holm's specimen has a marked sinus with small tooth on the palatal slab, a very inset basal tooth, less inset basal fold, a slight swelling on the columella margin and a deep columella lobe with rounded protuberance. Van Bruggen (1969) has commented on the variation in *Gulella radius* and described a closely related species from Natal, Zululand.

<sup>1</sup> This was examined many years ago but cannot now be found. Two specimens from Gazi are labelled paratypes (BM 1911.10.12.146–147) but the original description definitely states 'Shimbi Hills'.



**Gulella shoaensis** sp. nov. Fig. 18

*Description:* Shell oblong, narrowly perforate, creamy white, glossy; spire produced, the sides slightly convex, the apex broadly rounded. Whorls  $6\frac{1}{2}$ , slightly convex, gradually increasing; first  $2\frac{1}{4}$  whorls more or less smooth save for fine scratch-like lines not visible at  $\times 25$ ; rest of whorls with rather irregular ribs which peter out on the body whorl above the aperture but reappear behind the peristome and extend over the back of the body-whorl save for the pinched area between the two pits; some spiral element is visible between the ribs in this basal area; on the third visible whorl there are about 20 ribs per mm reducing down to about 8–10 per mm on the body-whorl. Aperture ovate-quadrate with 5 marked teeth and a prominent internal columella lobe; the angular lamella is hollowed out on the right hand side; a convexity on the outer lip bears two processes, the lower of which corresponds to a deep pit behind the peristome. The upper process cuts off a fairly marked sinus to the right hand side of the angular lamella; there is a broad basal process situated slightly to the left of the middle and also corresponding to a pit behind the base of the peristome; the mid-process on the columella slopes very slightly downwards and partly hides the conspicuous margined lamella.

*Dimensions:* Height 5.55 mm, breadth 2.6 mm; height of aperture 1.85 mm, breadth 1.73 mm.

*Distribution:* Ethiopia, Shoa, 90 km W. of Addis Ababa, 2450 m, 13 Feb. 1969, Åke Holm 162 (Holotype in Natural History Museum, Stockholm).

*Remarks:* The single specimen found was accompanied by *Acanthinula* sp., *Afroconulus* sp., *Kaliella barrakporensis* (Pfeiffer), *K. iredalei* Preston, *Gulella simplicima* (Preston) and *Ptychotrema* (*Parrennea*) (see next). I have been unable to match it with any described species despite its very ordinary looking appearance. It is not like any of those listed in my key to the *Gulella* of N.E. Africa (Verdcourt 1980). In my key to the East African species (Verdcourt 1962) it keys straight to *G. soror* (Smith) but examination of the type of that species shows it has a more ellipsoid shape, a thinner more curved angular lamella, the upper outer lip process a mere nodule on the upper slope of the lower and the mid-columella process small and not projecting downwards.

**Ptychotrema** Mörch, 1852.

Subgenus **Parrennea** Pilsbry, 1919.

**Ptychotrema tschibindanum septentrionale** ssp. nov. Fig. 19.

*Description:* Shell oblong-cylindrical, slightly tapering to the base, particularly when viewed from the back or sides, imperforate but with an umbilical depression, probably very glossy in life, creamy white but doubtless transparent in fresh state; spire produced, the sides more or less straight and the apex broadly rounded. Whorls  $6\frac{1}{2}$ , increasing regularly, the second visible whorl about as long as the third, slightly convex with strong subsutural costae at about 14 per mm, mostly extending for only a very short distance and rest of whorl more or less smooth save for some growth lines and a few of the costae extended right across and also a few regular ribs behind the peristome; the suture lightly impressed, crenellated by the short costae. Aperture ovate, broadly rounded at the base, the outer margin slightly sinuate; peristome thick; two basic processes, one in the usual angular position which cuts off an almost perfectly circular and well-developed sinus together with the distinct rounded process on the outer lip; the angular lamella when viewed obliquely sideways is bilobed; a narrowly oblong lobe on the columella at top, which slopes at either end; there is a deep external furrow running backwards round the body-whorl from the outer lip process for about half a whorl and a slight indentation between the edge of this furrow and the edge of the umbilical depression.

*Dimensions:* Height 2.8 mm, breadth 1.27 mm; height and breadth of the aperture 0.93 mm.

*Distribution:* Ethiopia, Shoa, 90 km W. of Addis Ab'aba, 2450 m, 13 Feb. 1969, Åke Holm 162 (Holotype in Natural History Museum, Stockholm).

*Remarks:* This is quite different in size, shape, extent of the external furrow and presence of a labral tooth from *P. somaliense* Verdc. (Verdcourt 1961) the only other *Parentnea* known from Ethiopia and Somalia. Adam & Van Goethem (1978) have revised the subgenus *Parentnea* and it seems clear from their figures that the closest affinity is with *P. tschibindanum* Pilsbry & Cockerell. With only a single specimen to hand not live-collected I have hesitated to give it specific rank since the variation shown by this species is very considerable. Nevertheless the form of the columella fold is rather different and the locality far distant. Notice of the occurrence of this taxon seems very necessary for zoogeographical reasons. It is hoped that fresher material will become available so that more adequate comparisons may be made.

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## REVIEW

*Biology of Opisthobranch Molluscs: Volume 2.* By T. E. Thompson and G. H. Brown. Published by the Ray Society, London in 1984. pp 229, 41 plates, 40 text figures, 98 distribution maps, 107 line drawings of British naked Opisthobranchs. ISBN 90 3874 180. Price £39.

The first volume of *Biology of Opisthobranch Molluscs* (Thompson 1976) begins with chapters on Classification and Affinities, Locomotion, Food and Feeding, Defence, Reproductive Organs, Development, Larval Biology and Life Cycles. The second half of Volume 1 deals with British opisthobranch species of the orders Bullomorpha, Aplysiomorpha, Pleurobranchomorpha, Acochliidae, and Sacoglossa (=Ascoglossa).

Volume 2 (Thompson and Brown 1984) continues straight on from the first with an account of 108 British species of Nudibranchia, an order which includes some of the loveliest sea creatures. A more precise and informative table for both volumes would be *British Opisthobranch Species*, for the main theme of both volumes is British species, their classification, descriptions, and biology.

T. E. Thompson has the bold, roving spirit of an Elizabethan sea-captain. For more than twenty years he has made annual voyages to the distant shores of America, Australia, Africa, the far East, and the Mediterranean. Each year he has returned with new species, changes in classification, and interesting observations on the biology of opisthobranchs—proofs of vast expertise and sound judgement. He is justly regarded as a leading authority on world opisthobranchs. The junior partner Gregory Brown, is a good artist and a well-trained zoologist—a rare combination! He is a keen collector of nudibranchs and has carefully observed the living species which he has faithfully depicted in Volume 2. Recently he revised the *Doto* complex that Lemche left. Both authors have successfully collaborated in a field guide, *British Opisthobranch Molluscs* (No. 8 in the Linnean Series). By their talents and experience they are well-equipped to write a work of the high standard expected by the Ray Society.

The Ray Society was founded in 1844 by a group of British zoologists to promote and fund the publication of important works, mainly about the British fauna. Their first publication was *A Monograph of the British Nudibranchiate Mollusca* by Alder and Hancock (1844–1855). Their descriptions were far in advance of the time and where it was illustrated by beautiful chromolithographic plates. It would have been interesting if Thompson and Brown had written a chapter comparing Volume 2 with Alder and Hancock's monograph. By this chapter we could have been informed what new species had been discovered, what changes in classification and advances in nudibranchology have been made since the days of Alder and Hancock. The production of their monograph almost exhausted the funds of the Ray Society. With the wisdom of hindsight, the Society have priced Volume 2 at £39 a copy.

In general plan the volume resembles a German *Handbuch*. It is attractively produced, splendidly illustrated, and the style is simple and direct. Malacologists will find it an indispensable modern reference work. A collector could identify a British nudibranch and learn much about its biology by the use of this book. Although there is a very comprehensive reference list some research workers might wish for more details and discussion in the text.

In the present century opisthobranch specialists have continued to find new opisthobranch species. They have been so successful that the number of opisthobranch species has almost doubled. Some specialists have described new species almost entirely by external features. Others have restricted observations on internal anatomy to descriptions of the radula. A glance through Volume 2 shows that 19 of the 40 text-figures and 4 of the plates illustrate teeth details. There are no text figures of complete alimentary or reproductive systems. So meagre is the information given in the literature that if Thompson and Brown had decided to write Volume 2 in the academic style exemplified by *British Prosobranch Molluscs* (Fretter and Graham 1962) they would have found the task almost impossible. Nevertheless they might have included 2 or 3 text-figures illustrative of reproductive details *pour encourager les autres*.

The colour plates were produced from water-colours by Gregory Brown. Large species look strikingly effective against a black ground, which also enhances the delicate colours of smaller species. Brown's 98 line drawings of naked opisthobranchs are excellent. They show a patient attention to detail and a natural representation of the living species that is pleasing to zoologists. They will be a valuable aid to identification. Dichotomous keys are given, but the beginner would be well advised to accompany the experts of the Conchological, Malacological, Porcupine Societies on their field meetings and learn to identify a number of species before relying on keys.

Volume 2 will remain the standard reference work in British Nudibranchs for many years. It is hoped that the authors, after about two decades, will write a *Supplement* to bring their work up-to-date.

TOM GASCOIGNE



# THE DISTRIBUTION AND HABITAT PREFERENCES OF FOUR SPECIES OF HYDROBIIDAE IN EAST ANGLIA

A. J. CHERRILL<sup>1,2</sup> AND R. JAMES<sup>1</sup>

(Accepted for publication, 18 May 1985)

*Abstract:* 119 brackish water habitats up tidal stretches of rivers and along a 220 km strip of coastline in East Anglia were searched for *Hydrobia ventrosa* (Montagu) and *H. neglecta* Muus. The presence of *H. ulvae* (Pennant) and *Potamopyrgus jenkinsi* (Smith) was also recorded. The number of sites containing *H. ulvae* was 47, *P. jenkinsi* 32, *H. ventrosa* 25 and *H. neglecta* 11. This represents an approximately four fold increase in known sites for the last two species in the British Isles. The salinities of sites recorded for the *Hydrobia* species overlap considerably. All four species may be found in non-tidal brackish dykes and lagoons. However *H. ventrosa* and *H. neglecta* show a strong preference for shallow nontidal waterbodies, whereas *H. ulvae* is closely associated with tidal habitats. *P. jenkinsi*, in this study, exhibited a preference for nontidal dykes of low salinity.

## INTRODUCTION

The distribution of *Hydrobia ulvae* and *Potamopyrgus jenkinsi* in the British Isles are well known. However, *H. neglecta* and *H. ventrosa* are poorly recorded. This is partly attributable to the recent discovery of *H. neglecta* by Muus (1963) and its omission from subsequent keys to British Prosobranchs (e.g. Graham 1971, Macan 1978). Kerney (1976) records *H. ventrosa* from nine 10 km squares and *H. neglecta* from twelve 10 km squares for the whole of the British Isles. Bishop (1976) lists 8 additional squares for *H. ventrosa*. In the past *H. neglecta* has undoubtedly been confused with *H. ventrosa* and possibly *H. ulvae*. As a result a large number of aggregate records of *Hydrobia* species await clarification (Kerney 1976). This survey goes some way towards rectifying the situation for East Anglia.

Previous studies of Hydrobiidae have considered salinity to be an important factor in determining their distribution (Bondesen & Kaiser 1949, Muus 1963, 1967, Fenchel 1975a, Bishop 1976, Fretter & Graham 1978). In this study salinity was measured and these data along with site classifications in terms of habitat type are presented. Previous records from within the study area are reviewed and the species distributions relative to salinity and habitat are compared with those reported in other studies.

## THE STUDY AREA

The area investigated was the coastal strip from Boston in Lincolnshire to Aldeburgh in Suffolk, together with tidal stretches of certain rivers. Fig. 1 and Table 1 describe the distribution of sampling sites. Many sites were seminatural lagoons or dykes to the landward side of sea defences. Such habitats are numerous in the study area particularly on the north Norfolk coast and around the Wash. Saltmarshes and mudflats extending to the seaward side of the sea walls were investigated where easily accessible. The remaining

<sup>1</sup> School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ.

<sup>2</sup> Present address: Department of Zoology, University of Liverpool, Liverpool, L69 3BX.

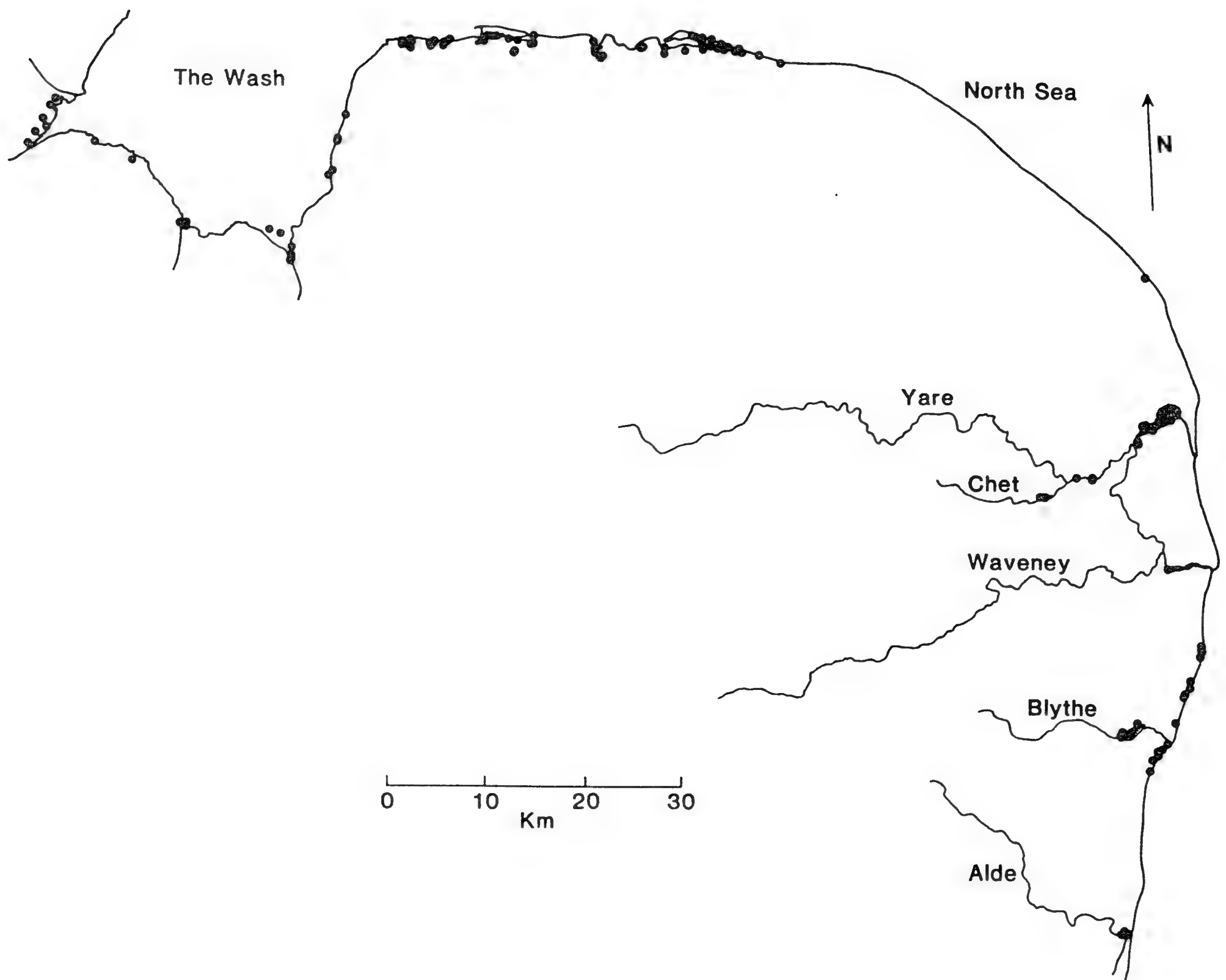


Fig. 1. Map of East Anglia showing the location of sampling sites.

samples were taken from the tidal reaches of the rivers Yare, Chet, Alde, and Blythe and adjacent dykes and marshes (Table 1).

The salinity of the sites ranged from 0‰ to 40‰. Bishop (1976) lists the prominent members of the invertebrate fauna associated with *H. ventrosa* and *H. neglecta* at a number of East Anglian locations grouped according to salinity.

#### METHODS

Potential sampling sites were identified by reference to 1:50000 Ordnance Survey maps. A total of 119 sites were sampled (Fig. 1). Samples were taken in July and October 1982 and in June 1983 (Table 1). A fine mesh long handled pond net was used to collect samples. When each site was first visited a rough estimate of abundance was made, based on the number of snails collected in 15 minutes (>500—very numerous, 100–500 common, <100—scarce, Table 1). Salinity measurements were made using a hydrometer, readings being adjusted for temperature (Harvey 1960).

Snails were tentatively identified from tentacular pigmentation and shell form. In all cases identification was then confirmed for each *Hydrobia* species at a site by examining the specific form of the penis (Muus 1967) in at least ten males. As *P. jenkinsi* is a parthenogenetic species over most of its distribution (Fretter & Graham 1978) it was

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TABLE 1

Locations of survey sites, types of habitat, presence and abundance of species and site salinities.

Site No.	Grid Ref.	Habitat Type	Species and Abundance				Salinity %		JUNE 1983
			JEN.	VEN.	NEG.	ULV.	JULY 1982	OCT.	
1	TF604 230	J					—	N.D.	—
2	TF606 231	C					N.D.	—	—
3	TF605 233	I				(2)	26·0	—	—
4	TF606 236	I				+	N.D.	—	—
5	TF608 236	B		(2)			10·0	9·0	—
6	TF593 253	C					19·0	—	—
7	TF585 254	H				(1)	N.D.	N.D.	—
8	TF491 265	A			(2)		25·0	29·0	—
9	TF497 266	C					N.D.	—	—
10	TF496 267	H				+	N.D.	—	—
11	TF647 314	F				+	N.D.	—	—
12	TF649 320	A				+	N.D.	—	—
13	TF445 325	B		(2)	(1)		35·5	28·0	—
14	TF407 345	A		(3)	(3)	(1)	24·5	20·0	—
15	TF652 346	A		(2)			11·5	8·0	—
16	TF343 347	A		(2)			17·0	10·5	—
17	TF653 348	A	(2)	(2)			6·0	8·0	—
18	TF346 352	A					N.D.	—	—
19	TF358 360	H				+	N.D.	—	—
20	TF355 364	B		(1)	(1)		22·0	20·0	—
21	TF664 374	D	(2)				2·0	—	—
22	TF368 385	H				+	N.D.	—	—
23	TF366 386	A		(2)	(1)		24·0	22·0	—
24	TF928 435	A	(3)				1·0	—	—
25	TF929 437	I				(3)	31·0	—	—
26	TF729 438	G					1·0	—	—
27	TF834 438	C	+				1·0	—	—
28	TF835 440	G					1·0	—	—
29	TF987 440	J					1·0	—	—
30	TF914 441	A					N.D.	—	—
31	TF750 442	A	+				0·0	—	—
32	TF989 442	G					1·0	—	—
33	TF727 443	F				(1)	34·0	31·0	—
34	TF966 443	H				(2)	—	31·0	—
35	TF764 444	K				(3)	N.D.	—	—
36	TF749 445	I				(2)	26·0	—	—
37	TF805 445	C	+				2·0	—	—
38	TF721 446	C	+				0·0	—	—
39	TF751 446	A				(3)	10·0	—	—
40	TF914 446	A					N.D.	—	—
41	TF964 446	H				(2)	—	32·0	—
42	TF805 447	G				(3)	N.D.	—	—
43	TF752 448	B				(3)	10·0	—	—
44	TF763 448	I				(2)	34·0	—	—
45	TF850 448	C	(2)				3·5	—	—
46	TF717 449	B		(1)		(2)	18·0	9·0	—
47	TF733 449	I				(3)	N.D.	—	—
48	TF829 449	A	+				0·0	—	—
49	TF836 449	C	(2)				2·0	—	—
50	TF854 449	A	(2)	(2)			13·0	—	—
51	TF766 450	F				(1)	40·0	27·0	—
52	TF853 450	F				(2)	N.D.	—	—
53	TF768 451	C	+				—	7·0	—
54	TF816 451	A	(3)				2·0	—	—



Table 1 continued.

Site No.	Grid Ref.	Habitat Type	Species and Abundance				Salinity %		JUNE 1983
			JEN.	VEN.	NEG.	ULV.	JULY 1982	OCT.	
55	TF820 452	G				+	N.D.	—	—
56	TF912 455	A				(2)	26.0	—	—
57	TG429 015	J					—	—	1.0
58	TG429 016	K		(2)			—	—	3.0
59	TG412 017	C	+				—	—	0.0
60	TG364 037	J	(1)				—	—	N.D.
61	TG474 051	E				+	N.D.	—	—
62	TG474 053	C	+				N.D.	—	—
63	TG489 064	C	(3)				N.D.	—	—
64	TG478 069	E					5.5	—	—
65	TG477 071	C	+				1.0	—	—
66	TG484 074	E				(1)	N.D.	16.0	—
67	TG504 074	C	(2)	(3)			5.0	—	—
68	TG508 075	E				(2)	23.0	—	—
69	TG493 076	I				(3)	—	—	N.D.
70	TG498 081	I		(2)		(3)	17.0	20.5	—
71	TG499 083	C		(3)			10.0	—	—
72	TG502 086	E				(1)	17.0	15.5	—
73	TG482 220	C					—	N.D.	—
74	TG109 436	A	(2)				0.0	—	—
75	TG009 442	C				(3)	17.0	—	—
76	TG085 442	B		(1)		(3)	36.0	27.5	—
77	TG044 444	C	(2)				2.0	—	—
78	TG045 445	I		(2)		(2)	17.0	14.0	—
79	TG059 445	C	(2)				0.5	—	—
80	TG029 446	A				(3)	14.0	—	—
81	TG068 447	B		(3)			30.0	—	—
82	TG029 448	A				(3)	17.0	—	—
83	TG045 448	G				(3)	—	—	N.D.
84	TG064 448	B					30.0	—	—
85	TG048 449	A	(1)	(2)			19.0	16.0	—
86	TG053 451	A		(3)			30.0	—	—
87	TG049 452	B					21.0	—	—
88	TG040 455	F				+	—	—	N.D.
89	TG030 457	I				(2)	—	—	N.D.
90	TG024 459	I				(3)	—	—	N.D.
91	TG030 459	I				(3)	—	—	N.D.
92	TG020 460	F				+	—	—	N.D.
93	TM453 555	C	(2)				—	9.0	—
94	TM457 556	E					—	N.D.	—
95	TM457 557	A	(3)				—	7.0	—
96	TM459 557	E				+	—	N.D.	—
97	TM463 557	A		(2)	(2)		—	13.0	—
98	TM485 723	B			(1)		31.5	23.0	—
99	TM487 732	C			(2)		17.5	14.0	—
100	TM493 737	B			(1)		30.0	22.0	—
101	TM496 742	C			(3)		17.5	—	—
102	TM498 743	B			(1)		29.0	23.0	—
103	TM501 747	I		(2)		(2)	23.0	25.0	—
104	TM452 756	J					4.0	—	—
105	TM452 757	E				(2)	N.D.	—	—
106	TM454 759	E				(2)	15.0	—	—
107	TM472 768	E					8.0	—	—
108	TM511 769	A	(2)	(2)			8.0	—	—
109	TM518 794	A					1.0	—	—
110	TM519 798	B	(2)				3.5	—	—
111	TM523 807	A	(3)	(3)			9.0	—	—

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Table 1 continued.

Site No.	Grid Ref.	Habitat Type	Species and Abundance				Salinity %		
			JEN.	VEN.	NEG.	ULV.	JULY 1982	OCT.	JUNE 1983
112	TM533 830	A					5.0	—	—
113	TM535 836	B		(2)		(3)	11.5	3.0	—
114	TM536 840	A		(1)			26.0	25.0	—
115	TM535 842	A	(1)				6.0	—	—
116	TM535 845	C	+				0.0	—	—
117	TM503 926	K	+				N.D.	—	—
118	TM377 996	K					—	—	N.D.
119	TM383 996	K	(3)				—	—	N.D.

Types of Habitat—nontidal: A Lagoons, B Pools, C Dykes, D Rivers; tidal: E Riverine mudflat, F Coastal mudflat, G Saltmarsh creek, H Exposed saltmarsh, I Sheltered saltmarsh, J Rivers, K Reedmarsh.

Species and Abundance: JEN.=*P. jenkinsi*, ULV=*H. ulvae*, NEG.=*H. neglecta*, VEN.=*H. ventrosa*, (1) Numerous, (2) Common, (3) Scarce, + Abundance not estimated.

Salinity (%): ND=Salinity not recorded, (—)=not visited.

identified from its distinctive shell form and tentacular pigmentation alone. A minimum of ten suspected *P. jenkinsi* were dissected to check for the presence of males and possible confusion with *H. ventrosa*. Populations containing keeled individuals (Bondesen & Kaiser 1949, Fretter & Graham 1978) were noted.

## RESULTS

The species present at the 106 sites sampled in 1982 and the 13 sites sampled in 1983 are given in Table 1. *H. ulvae* was recorded at 47 sites (39.5% of all sites), *H. ventrosa* at 25 sites (21.0%), *H. neglecta* at 11 sites (9.2%) and *P. jenkinsi* at 32 sites (26.9%). Only 22 sites (18.5%) failed to yield any hydrobiids. Sympatry occurred at 17 (17.5%) of the 97 inhabited sites. *P. jenkinsi* and *H. ventrosa* were recorded as sympatric six times, *H. ventrosa* and *H. neglecta* four times and *H. ventrosa* and *H. ulvae* six times. All three *Hydrobia* species were recorded together at a single site (site 14, Table 1).

The frequencies with which sites of different salinity were occupied by each species in July and October 1982 are shown in Fig. 2. Mean salinities ( $\pm$ S.E.) for each month and species are given in Table 2. At all but four sites (numbers 8, 17, 70 and 103 Table 1) salinities were lower in October than in July. The ranking of the species in order of increasing average salinity however is the same in each month (Table 2). Despite this pattern *H. ulvae* and *H. ventrosa* occur in wide salinity ranges which coincide almost completely (Fig. 2). *P. jenkinsi* and *H. neglecta* occupy more restricted salinity ranges. That of *H. neglecta* is spanned by the ranges of *H. ulvae* and *H. ventrosa*, whereas *P. jenkinsi* exhibits moderate overlap with only *H. ventrosa*. Although there is considerable overlap in the field salinities occupied by these species they are less similar in terms of their habitat preferences.

Eleven categories of habitat were identified, four nontidal (A–D) and seven tidal (E–K) (Table 1). Lentic non-tidal waterbodies were the most frequently sampled. They have been separated into those shallower than 0.6 m (Pools, B) and those of greater depth (Lagoons, A). Habitat type C (Dykes) contained still or slowly flowing water when visited but may periodically experience lotic conditions.

The frequencies with which the species occur in each habitat type are given in Table 3. *H. ulvae* was recorded from nine habitat types, *P. jenkinsi* and *H. ventrosa* five each, and *H.*

TABLE 2

Mean salinities of sites occupied by each species in July and October 1982

Species	July			October		
	$\bar{x}$	SE	N	$\bar{x}$	SE	N
<i>P. jenkinsi</i>	3.76	0.99	23	9.4	1.69	5
<i>H. ventrosa</i>	17.52	2.13	23	16.38	1.88	17
<i>H. ulvae</i>	22.14	1.86	22	20.88	2.52	13
<i>H. neglecta</i>	25.65	1.86	10	21.14	1.62	10

$\bar{x}$  mean ‰, SE=standard error, N=number of salinity measurements in sample.

*neglecta* three. Non-tidal sites make up 57.14% of all sites sampled. However, all of *H. neglecta*'s populations, 90.6% of *P. jenkinsi*, 84.0% of *H. ventrosa*'s, and 23.4% of *H. ulvae*'s were found in non-tidal sites. *P. jenkinsi*, *H. ventrosa* and *H. neglecta* each exhibit a statistically significant association with non-tidal sites ( $P < 0.001$ ,  $P < 0.01$ ,  $P < 0.01$  respectively). *H. ulvae* is positively associated with tidal sites ( $P < 0.001$ ).

The proportion of sites of each habitat type occupied by each of the four species are shown in Fig. 3. All four species occur in lagoons although for none is it the most preferred habitat. Within non-tidal habitats none of the four species shows a statistically significant association with lagoons ( $P > 0.10$  for each species). *P. jenkinsi* shows a significant positive association with dykes ( $P < 0.01$ ), and is negatively associated with pools (significant at  $P < 0.01$ ). In contrast, of the non-tidal habitats, each of the *Hydrobia* species is most strongly associated with pools and is least frequent in dykes (Fig. 3, Table 3). None, however, show a significant association with pools and only *H. ventrosa* shows a significant negative association with dykes ( $P < 0.01$ ). The consistency of the pattern between the *Hydrobia* species suggests the data are biologically significant if not statistically so in every case (Fig. 3).

Not surprisingly of the 17 sites supporting sympatric populations 13 are lagoons or pools. These habitats contained all sympatric populations of *H. ventrosa* and *H. neglecta* and all but one case of coexistence between *P. jenkinsi* and *H. ventrosa*. *H. ulvae* and *H. ventrosa* were found to coexist in pools, areas of sheltered saltmarsh and one lagoon (where *H. neglecta* was also present).

Each of the populations of *H. ventrosa* occurring on sheltered saltmarsh were sympatric with *H. ulvae*. These sites (particularly sites 70 and 103, Table 1) are vulnerable to inundation at high tides. Between July and October 1982 the population of *H. ventrosa* at site 70 appeared to go extinct and its numbers at site 103 declined dramatically. The absence of empty shells and the higher October salinities at these two sites (Table 1) indicated recent tidal inundation. Elsewhere numbers of *H. ventrosa* did not change noticeably over the same period. Thus although *H. ventrosa* shows a modest association with sheltered saltmarshes this is perhaps a marginal habitat for the species. This view is reinforced by its pronounced association with non-tidal habitats.

Only a single population of *P. jenkinsi* (site 67) was found to contain individuals with keeled shells and no males were recorded at any site.



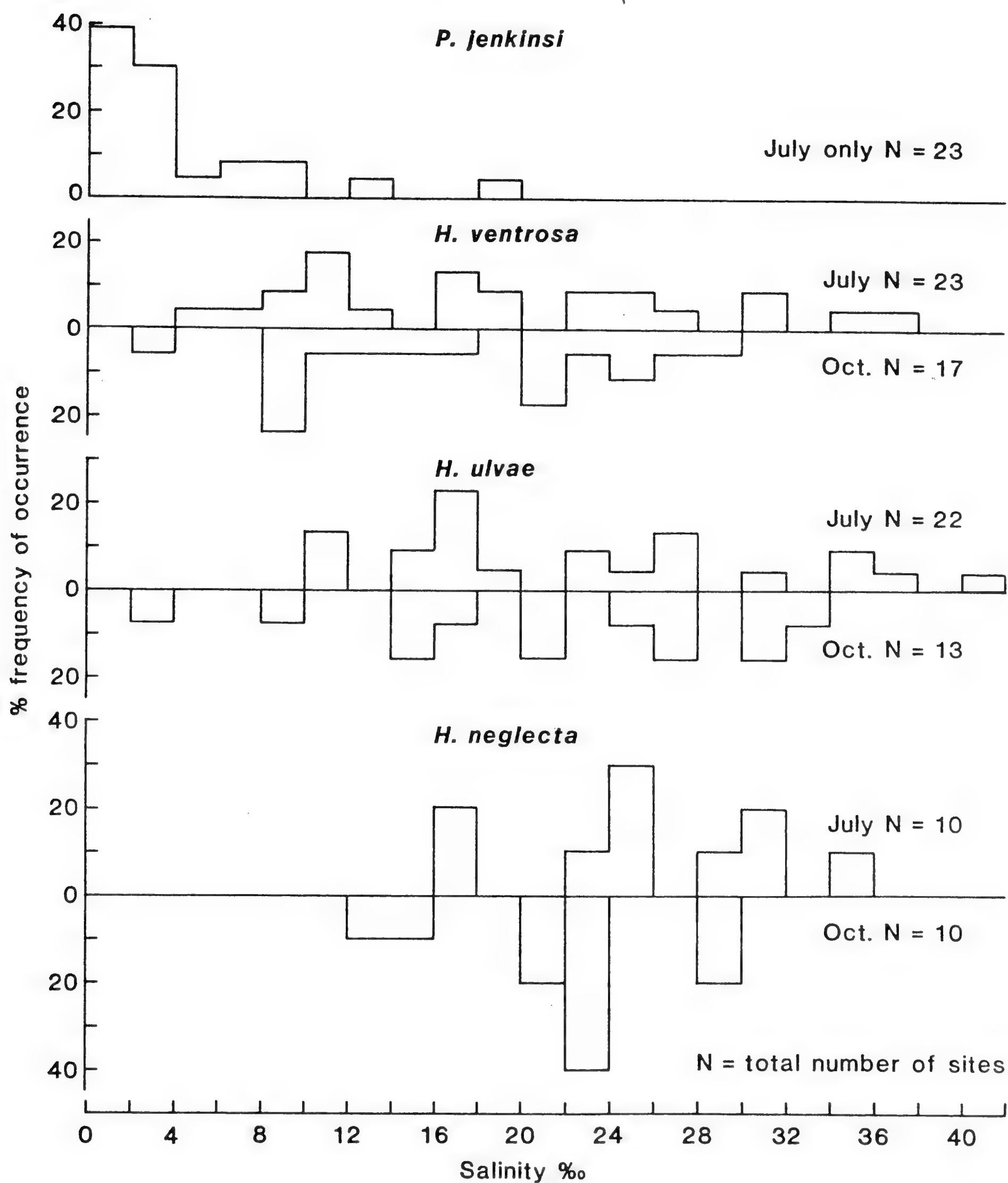


Fig. 2. Frequency of sites (expressed as %) occupied by each species in relation to site salinity. (Insufficient data, N=5, for *P. jenkinsi* in October).

## DISCUSSION

### *Previous Records*

These species clearly represent an important component of the brackish water fauna in East Anglia. Prior to this study *H. ventrosa* and *H. neglecta* were significantly under-recorded. Doubtless this remains true nationally. The number of segregate records of *H. ventrosa* has been increased from 6 to 25 including records for 6 new 10 km squares. The increase for *H.*

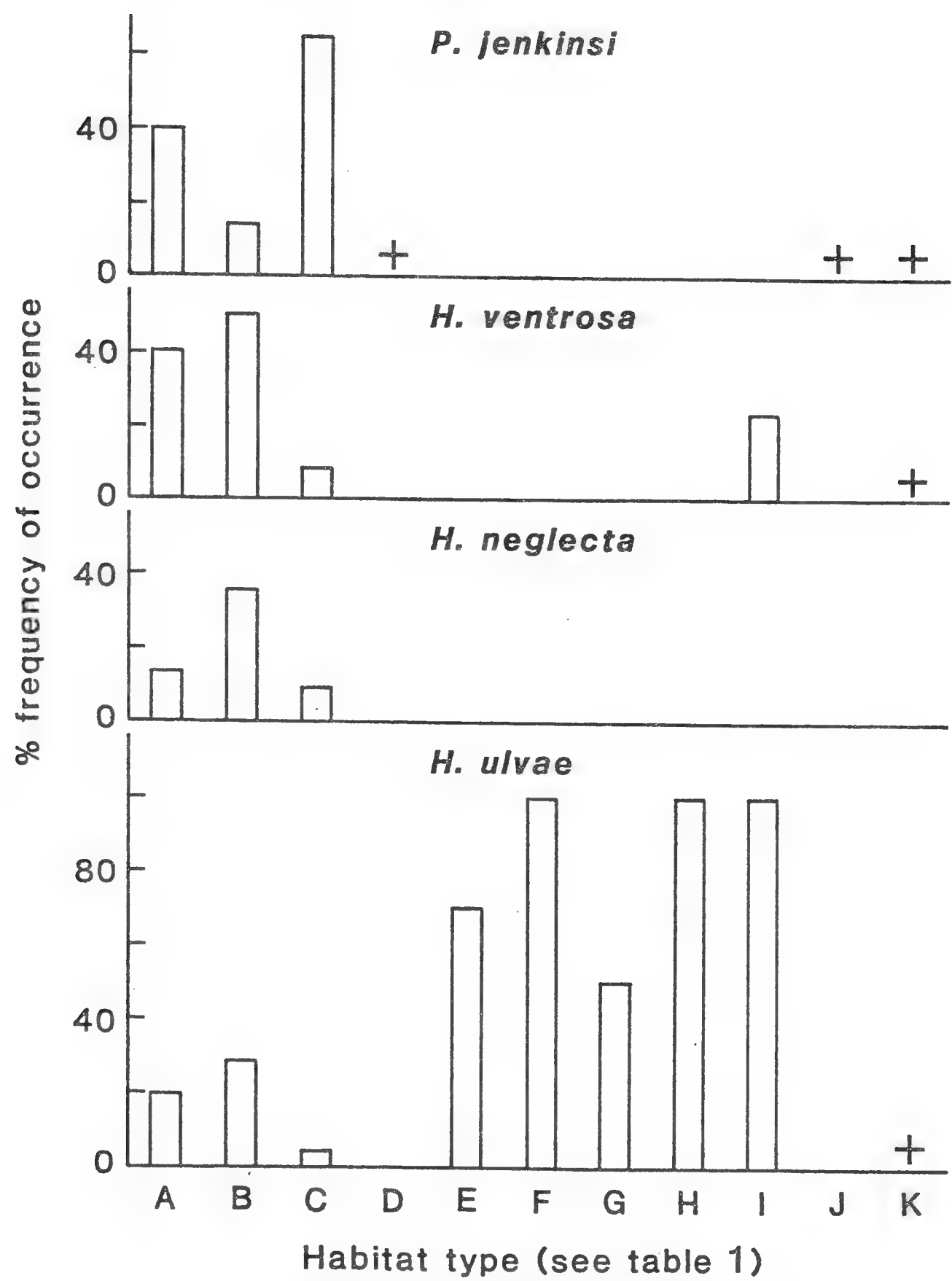


Fig. 3. Frequency of sites (expressed as %) of each habitat occupied by each species. (Insufficient data,  $N \leq 5$ , from sites D, J and K, + indicates presence of species).

TABLE 3

Frequency of occurrence of each species at sites of each habitat type for all samples. (Habitat types see table 1)

Species	A	B	C	D	E	F	G	H	I	J	K	Total
<i>P. jenkinsi</i>	12	1	15	1						1	2	32
<i>H. ventrosa</i>	12	7	2						3		1	25
<i>H. neglecta</i>	4	5	2									11
<i>H. ulvae</i>	6	4	1		7	6	3	6	13		1	47
Spp absent	5	2	4		3		3			4	1	22
Total number of sites	30	14	23	1	10	6	6	6	13	5	5	119

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TABLE 4

Mean salinities occupied by each species in (A) lagoons (B) pools for combined July and October 1982 samples

Species	Habitat A—Lagoons			Habitat B—Pools		
	$\bar{x}$	SE	N	$\bar{x}$	SE	N
<i>P. jenkinsi</i>	6.79	1.62	14	3.50	—	1
<i>H. ventrosa</i>	16.34	1.69	19	19.96	3.03	13
<i>H. ulvae</i>	18.58	2.51	6	16.43	4.39	7
<i>H. neglecta</i>	22.50	1.90	7	26.40	1.61	10

$\bar{x}$  mean %, SE=standard error, N=number of salinity measurements in sample.

*neglecta* is more modest with records increasing from 3 to 11 including 2 new 10 km squares. The recorded distributions of *H. ulvae* and *P. jenkinsi* (Kerney 1976) have not been extended. In common with other studies in the British Isles and Denmark (Bishop 1976, Muus 1963 & 1967, Fenchel 1975a) we found *H. neglecta* to be the rarest and *H. ulvae* the most widespread of the *Hydrobia* species.

A number of populations identified by previous authors could not be located. Notably neither record of *H. neglecta* in Norfolk shown in Kerney (1976) is currently accurate. One of these, at Titchwell, was recorded in 1970 by Williams (1972) but was extinct by 1973 (Bishop 1976). The second record, at Arnold's Marsh, Cley (site 84, Table 1) is based on empty shells only (Kerney pers. comm.). No hydrobiids were found at this site. However specimens of *H. ventrosa* were found in adjacent waterbodies (sites 81 and 86, Table 1) and in abundance at three nearby sites (76, 78 and 85, Table 1). Since shell form is an unreliable character (Muus 1967, Bishop 1976) it is likely that the original specimens were misidentified.

One population of *H. ventrosa* discovered by Bishop (1976) at site 53 (Table 1) could not be found. This population may have become extinct or be very localised. *H. ulvae* at site 23 has certainly become extinct since Bishop's visit. The *Hydrobia* species distributions appear far from static but older records are inadequate to test this idea. Most date back to the end of the last century (Mayfield 1896, Anon 1938, Biggs 1969 and Hammond 1971). None prior to Bishop (1976) are sufficiently precise to be useful in this respect.

#### Habitat Type and Salinity

Muus (1963) proposed that the hydrobiids can be arranged in order of their preferences for increasing salinity as follows: *P. jenkinsi*, *H. ventrosa*, *H. neglecta*, *H. ulvae*. Data presented by Muus (1967), Fenchel (1975a) and Bishop (1976) are supportive. However in this study the average salinity recorded for *H. ulvae* is lower than that for *H. neglecta* (Table 2). This probably results from our bias towards the sampling of habitats thought suitable for *H. ventrosa* and *H. neglecta*, combined with difficulties in obtaining salinity measurements from tidal sites (see Table 1). As seen in other studies (Muus 1967, Fenchel 1975a, Bishop 1976, Fretter & Graham 1978) there is considerable overlap in the salinities occupied by the species. Comparison of the ranges occupied by each is perhaps more meaningful than the use of mean values.

In comparison with salinity the types of habitats in which the species occur have received little attention. Muus (1967) and Fenchel (1975a) associated *H. ulvae* with open, exposed sites experiencing a relatively high degree of water turbulence. They associated *H. ventrosa* and *H. neglecta* with relatively sheltered, lentic sites. The same general pattern has



been noted in the British Isles (Fretter and Graham 1962, 1978) and the Netherlands, though *H. neglecta* is as yet unrecorded in the latter country (Butot, pers. comm.). These observations are consistent with the more quantitative picture presented here.

The most important habitat feature in East Anglia appears to be whether or not a site is tidal. Muus (1967) proposed that *H. ventrosa* and *H. neglecta* are intolerant of water movement whereas *H. ulvae* has a preference for it. Water movement is undoubtedly an important characteristic of the rivers and tidal habitats in East Anglia. The development of *H. ulvae* suggests that it is suited to open, lentic environments since it possesses a planktonic veliger larva (Pilkington 1971, Chatfield 1972). In contrast *H. neglecta* and *H. ventrosa* lack a specialised dispersal phase in their development (Muus 1967, Lassen 1979). A lower dispersal ability is typical of lagoonal species in comparison to their more marine congeners (Fretter & Graham 1962, Barnes 1980).

*P. jenkinsi* is said to prefer flowing water (Fretter & Graham 1978). However, in this study its apparent habitat preferences can be explained by its salinity requirements. It is physiologically intolerant of salinities above 20.0‰ (Muus 1967, Fretter & Graham 1978). All dykes and most lagoons have salinities below 20.0‰ whereas most pools have salinities above 20.0‰ (Table 1). *P. jenkinsi* is most strongly associated with dykes, also occurs in lagoons but is rare in shallow pools (Fig. 3).

Separation of the relative importance of salinity and habitat type in determining the *Hydrobia* species' distributions represents an interesting problem. We believe the typical association of *H. ulvae* with the highest salinities (Muus 1967, Fenchel 1975a, Fretter & Graham 1978) can be explained by its having a preference for open, tidal habitats rather than high salinities per se. In the Limfjord site exposure and water turbulence are positively correlated with salinity (Muus 1967, Fenchel 1975a). As a result the relative roles of the species' salinity and habitat preferences cannot be assessed from published studies (Muus 1967, Fenchel 1975a, b) of the area. The classification of sites according to habitat type permits this in East Anglia. In Table 2 tidal habitats are under-represented in the calculation of the mean salinities (see Table 1) and it is probably for this reason that *H. ulvae* does not take its expected position relative to *H. neglecta*. It should be noted that in lagoons *H. ulvae*, on average, occupies lower salinities than *H. neglecta*, and in pools lower salinities than both *H. neglecta* and *H. ventrosa* (Table 4). This strongly suggests *H. ulvae*'s widely accepted 'preference' for relatively high salinities is, in fact, a reflection of a widespread correlation between its preferred habitats and high salinities.

There is also evidence that correlations between habitat type and salinity may influence the range of salinities occupied by *H. ventrosa*. In the Limfjord this species rarely occurs in salinities above 20.0‰ (Muus 1967, Fenchel 1975a). In East Anglia it frequently occurs in higher salinities (Fig. 2). The species' preference for sheltered habitats however is seen in both regions (Muus 1967, Fenchel 1975a, Fig. 3). The salinities exhibited by such habitats differ between the two. In east Anglia 39.5% of lagoons and pools have salinities of over 20.0‰. In the Linfjord sheltered sites with salinities above 20.0‰ are rare (Muus 1967, Fenchel 1975a).

Both Muus (1967) and Fenchel (1975a) note that while the *Hydrobia* species' salinity preferences relative to one another are constant from area to area, the absolute salinities occupied by each varies. Regional variations in the salinities exhibited by the species' preferred habitats may be the explanation.

The difference between the salinities occupied by *H. neglecta* and *H. ventrosa* however cannot be accounted for by the differences in their habitat requirements (Fig. 3, Table 4). Nor does it result from differences in their fundamental niches since these are more-or-less identical (Muus 1967, Fretter & Graham 1978). Fenchel (1975a) suggests that the *Hydrobia* species' apparent salinity preferences are mediated by variation in their relative competitive abilities with salinity (i.e. that *H. ulvae* is competitively superior at the highest

salinities, *H. ventrosa* at the lowest and *H. neglecta* at intermediate). *H. ulvae* would again be expected to occur in the highest salinities not only overall but also within habitat types. This is not the case (Tables 2, 4). However, observations for *H. ventrosa* and *H. neglecta* are consistent with Fenchel's hypothesis. Fenchel and Kofoed (1976) have demonstrated in the laboratory that there is the potential for competition between all three *Hydrobia* species in the field. The actual significance of competition for their distributions has yet to be demonstrated. Evidence for competitive character displacement has been recorded from both regions (Fenchel 1975b, Cherrill & James unpub.) but this is open to other interpretations (Cherrill & James in prep.).

## ACKNOWLEDGEMENTS

Thanks are due to Sue Mitchel who drew the figures and to M. Begon who read the manuscript. M. P. Kerney and L. J. M. Butot generously made information available. The survey was made possible by the loan of transport by A.J.C.'s parents.

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## REVIEW

*The Freshwater Mollusca of Northern Africa; Distribution, Biogeography and Palaeoecology.* By Dirk Van Damme. Dr. W. Junk Publishers, 1984. 164 pp., 144 text-figures. Hfl. 150 (about £35). ISBN 90 6193 502 4.

Ever since the monumental work of Pilsbry and Bequaert (1927) with its quite remarkable coverage of published names of African freshwater molluscs, still an unsurpassed tool, this group has been rather well-served with literature, at least by comparison with the land molluscs. Mandahl-Barth's book on the Uganda fauna and many revisionary papers, further revisions and popular leaflets from the Danish Bilharziasis Laboratory and particularly David Brown's recent manual have made identification of freshwater molluscs possible. This literature is of course basically due to the importance of water-snails in transmitting various diseases. However, most of it omits the species of that part of Africa falling within the Palaearctic region; the same area is also not dealt with in works devoted to the Mediterranean area. Van Damme's book, volume 25 in a general series 'Developments in Hydrobiology' fulfils a real need and complements the other works, particularly as it includes coverage of the bivalves, not treated in Brown's work. The emphasis of the book is the geologically recent history of the Sahara and the value of molluscan studies in understanding its fascinating climatic vicissitudes; it does, however, cover a much more extensive field.

A brief history of collecting in northern Africa as a whole precedes the main treatment and as usual Bourguignat has complicated matters by excessive splitting. Pallary following later emulated him to no small extent. Part one occupies over half the book and is a review of the species, a compilation and not a revision which in some groups e.g. Hydrobiidae is much-needed. Species in 49 genera are dealt with. The descriptions are brief but line drawings are given of each. These are adequate save in the case of *Pisidium* where the hinge details could be clearer. Fig. 112 purporting to depict *Sphaerium lacustre* is not similar to any specimen I have seen being too inflated. The Recent and detailed Late Pleistocene—Holocene distributions are given together with a map. Many species are now very restricted and the author points out that almost all are under threat from pollution. Some synonymy is given and for some species extensive bionomic details under the remarks. Original places of publication are not given for either the correct names or the synonyms and for these Pilsbry and Bequaert is still required. Much space is saved by these omissions and in any case those who need such details know where to find them. The type localities are, however, given for each species.

Part two details the distribution of freshwater molluscs over the whole of Africa succinctly, region by region, in a way which complements rather than replaces Brown's account. It confirms only what is already known save that the Palaearctic-Ethiopian demarcation line is defined in much more detail. Parts three and four are I think the most valuable and deal with Cretaceous and Tertiary history, including evidence available from beyond the strict region concerned, and with the Quaternary fauna of northern Africa respectively. They give a much-needed summary of recent work. I was surprised at the amount of material now available. In the first half of the Cretaceous the fauna was rich, particularly in bivalves, and has declined since; in particular that universal extinction which struck at the end of the Cretaceous. From the Palaeocene up to the early Miocene Ampullariids flourished in extensive swamps, a conclusion I also reached when dealing with Kenya deposits. The great and rather puzzling difference between the fauna of much of northern Africa, derived almost entirely from Europe and Asia when the Atlas chain was geologically new, and the Afrotropical fauna is partly explained by a shallow sea existing before the Mid-Miocene; the Afrotropical species were later unable to oust species which had become well-adapted to hot often brackish conditions. The development of deep lakes had a great influence on mollusc evolution. The unique fauna of Lake Tanganyika may not have been the result of gradual evolution over a long period as generally believed but due to bursts of speciation followed by periods of stability. This follows studies of the Pliocene Lake Kairo and Lake Turkana (Williamson's punctuated equilibrium model) (Figs. 141 and 142 show this pictorially). During the Pliocene the radiation of the Pulmonate species, now so common, started. Except for further extinctions there has been little change since. Part 4, the most interesting of all, deals with times slowly more and more dominated by man and will thus be that most important to anthropologists and archaeologists. In northern Africa it is the history of unstable environments with repeated colonizations and extinctions mirroring numerous climatic changes. This results in little evolutionary change and the most recent speciation is early Pliocene or earlier. Interesting is the fact that the present Sahara had its initiation during the late Pliocene. A short essay on dispersal modes contains the novel suggestion that Darwin's famous record of an adult *Anodonta* attached to a duck's foot might be the result of a practical joke—but of course quite without evidence.

A list of all the localities mentioned is very useful and correlated with the map fig. 144 (although this is not mentioned in either the map-caption or the list-heading although they are 12 pages apart). The 9 pages of



## REVIEW

bibliography are exhaustive and extremely valuable although the absence of Hamilton's Environmental History of East Africa (1982) is surprising. The two indexes seem complete.

There are rather too frequent misprints, many of the same kind involving double letters e.g. p. 39 'Connoly', p. 55 'neat', p. 95 'Ampulariidae', p. 97 'Gabiella', p. 104 'Quadrulla', p. 116 'Peudodiplodon', p. 136, 'Pre-Cambrium' and some oddities e.g. the hybrid English-French p. 53 and 105 'conchyologically', p. 112 'conchyological' also p. 2 'epigons' (surely used in the wrong sense). Still let us be thankful the text is in English! The use of italic and Roman script is somewhat erratic e.g. in the list of contents where some authorities are also missing—this right at the beginning of a book gives a bad impression and should have been picked up by readers. The abbreviation a.o. which appears in various places seems to mean e.g. but remains a mystery to me. One reference on p. 117 puzzles me; the author quotes Oswald in Verdcourt 1963 although Oswald was long dead when I wrote on the Miocene Mollusca of Rusinga etc. and he also makes reference to *Cleopatra amoena=ferruginea* but these are not mentioned in my paper. The reference is really to R. Bullen Newton's paper describing Oswald's material and the species concerned was claimed to be *C. exarata*.

Reviewers have mostly ceased their once perennial complaints about the price of books but 164 pages and no plates, not even black and white, for approximately £35 is I think very steep. What is more it just encourages illegal copying with the superb modern copiers now available for a fraction of the price. I know all the publisher's explanations of these prices by heart but am still not convinced that a wider sale which includes ordinary folk would not net more profit. Those who need this book will have to use institutional copies.

This aesthetically dull group does not attract many collectors but the extreme value of molluscs as climatic indicators means this book will be required reading for all interested in the climatic history of the Sahara from the Cretaceous right up to modern times and other parts of Palaearctic Africa.

BERNARD VERDCOURT

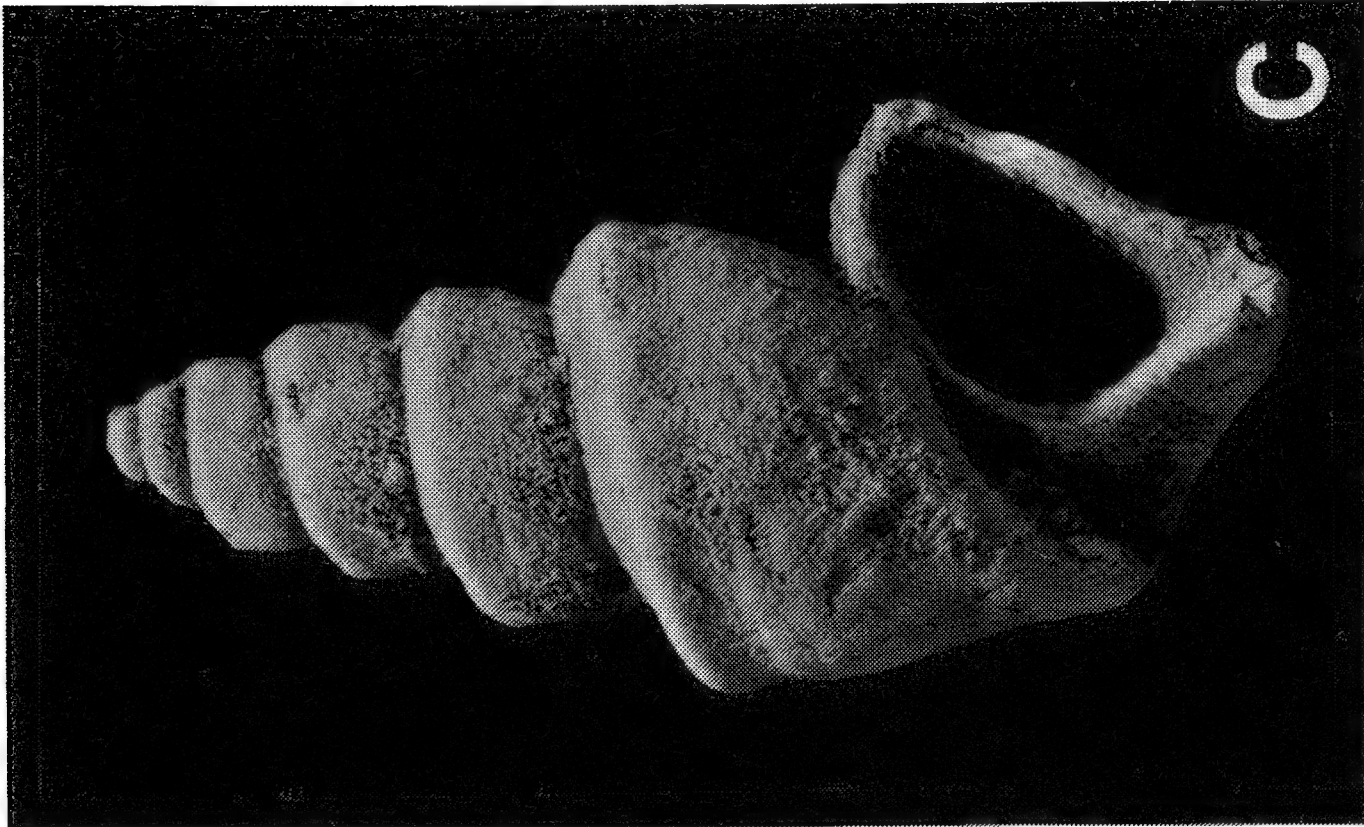
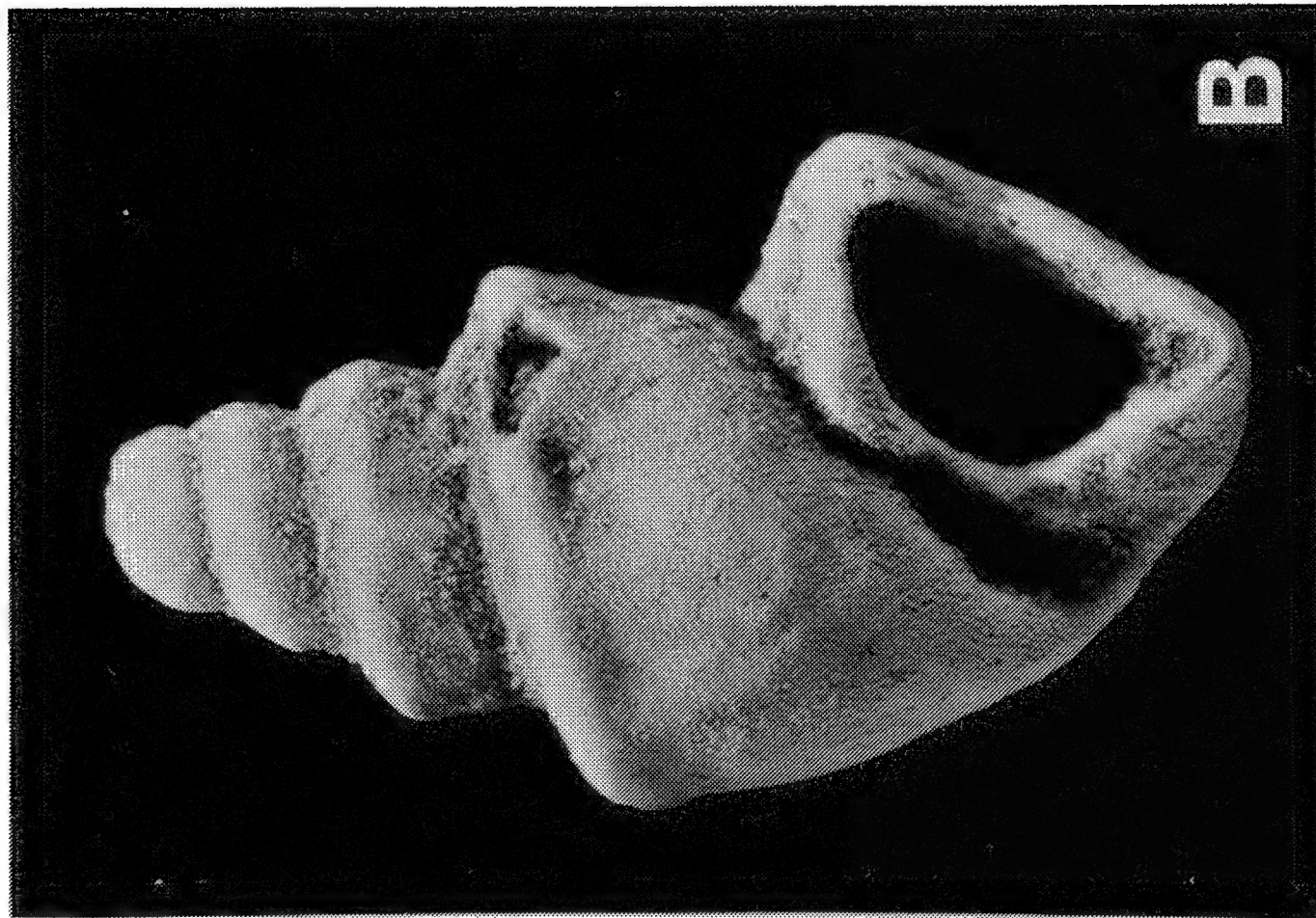
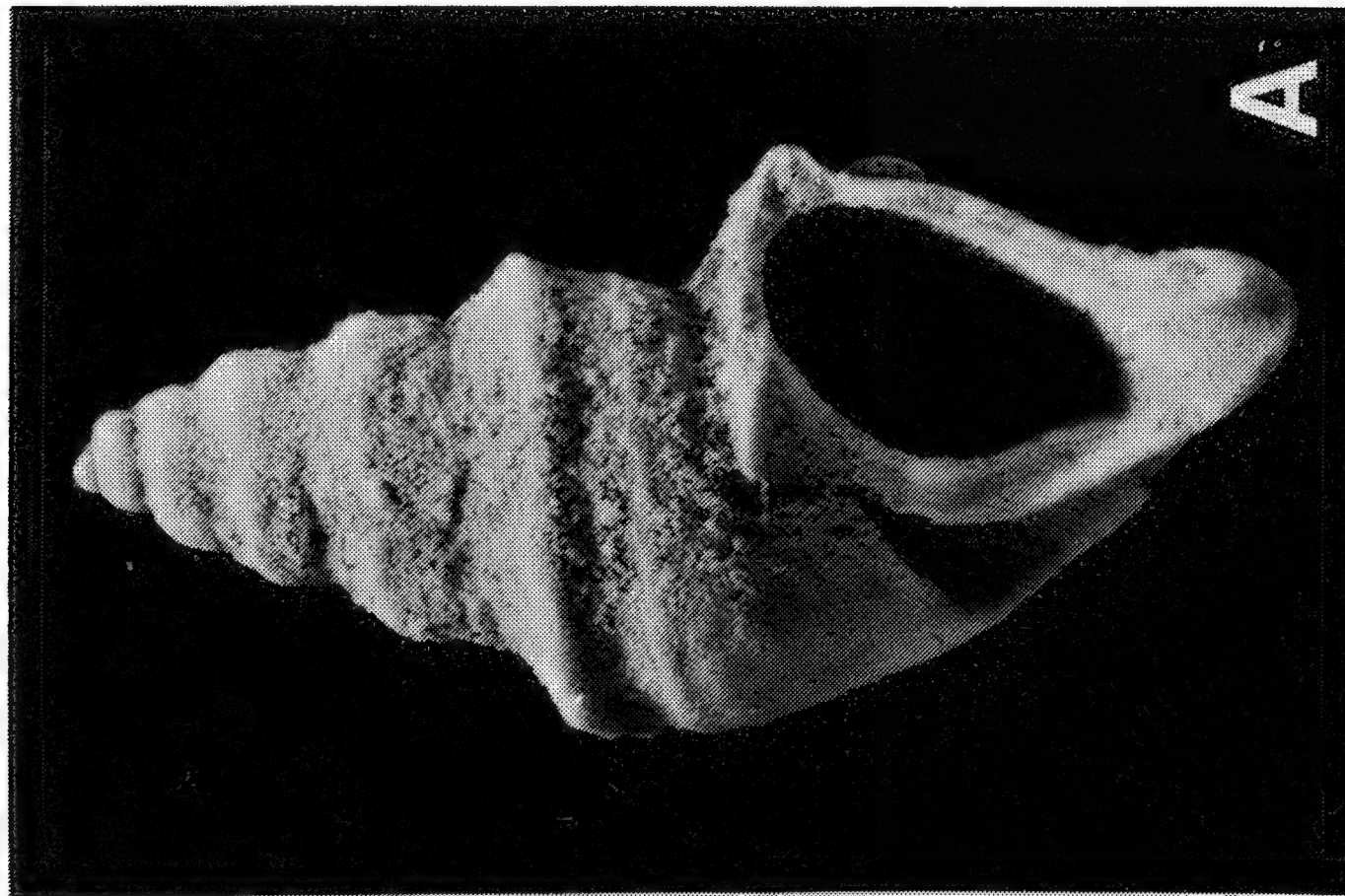


PLATE 13

Holotype (Fig. 2A) and paratypes (Figs. 2B and 2C) of *Potadoma lomewiensis* from late Cenozoic deposits of the western Turkana Basin, north Kenya. Specimens are (a) KNMI-WT 15609 in the collections of the National Museums of Nairobi, (b) specimen KNMI-WT 15610 in the same collection, and (c) specimen MCZ-29184 in the collections of the Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University.

# A FIRST RECORD OF *POTADOMA* (SWAINSON) (PROSOBRANCHIA: GASTROPODA) FROM EASTERN AFRICA

P. G. WILLIAMSON<sup>1</sup>

(Accepted for publication, 18 May 1985)

*Abstract:* Two recently discovered late Cenozoic faunas from the western Turkana Basin, north Kenya, have yielded a gastropod clearly referable to *Potadoma* (Swainson), a genus hitherto known only from west and central Africa. This first record of *Potadoma* from eastern Africa is of interest in demonstrating a drastic recent reduction of the range of the genus, particularly as the Turkana material has strong affinities with a sub-group of *Potadoma* known only at present from a restricted area of Cameroun, some 1800 miles to the west. The recent reduction in the range of *Potadoma* offers some interesting parallels with the late Cenozoic reduction in range of the mutelid bivalve *Pleiodon*, which also has a west and central African distribution at present, but which was also widely distributed in eastern Africa until recently. This record of *Potadoma* from the western Turkana basin may also provide useful paleoecological information regarding the important hominid-bearing deposits of the area.

## INTRODUCTION

Two faunas recently discovered in late Cenozoic deposits from the western Turkana Basin, north Kenya, have yielded a gastropod clearly referable to *Potadoma*, a genus hitherto known with certainty only from West and Central Africa. These faunas were recovered by Dr. F. H. Brown in the course of a stratigraphic reconnaissance undertaken for the Koobi Fora Research project of the National Museums of Kenya, and come from the area of the Lomekwi drainage on the western shores of Lake Turkana at approximately 3°50'N, 35°50'E. The faunas occur in fluvial sediments at two stratigraphic levels about 2 m apart, at the level of the Tulu Bor tuff, dated at about 3.2 Myr (Brown and Cerling 1982). These faunas have also yielded *Bellamyia unicolor* (Olivier), *Melanoides tuberculata* (Müller), and small specimens of *Cleopatra bulimoides* (Olivier).

Seventeen recent species of *Potadoma* are recognized in the most recent reviews of the genus by Mandahl-Barth (1967), of which *P. freethi* is the most widely distributed. The genus currently occupies several disjunct areas in West and Central Africa (see Fig. 1). The occurrence of *Potadoma* in the western Turkana Basin indicates that the African range of this genus was previously far more extensive than at present; the nearest modern occurrence of *Potadoma* is almost 500 miles to the west, in eastern Zaire. The present disjunct distribution of *Potadoma* in west and central Africa might suggest that the genus is indeed undergoing a reduction in range at present, and was formerly more widely distributed. In this connection, the shell morphology of the *Potadoma* material from Turkana is particularly intriguing. Modern representatives of the genus can clearly be divided into two groups on the basis of shell form and sculpture (Brown 1980). The most widely distributed group, exemplified by forms such as *P. freethi* (Gray) and *P. vogeli* (Binder) includes 13 of the 17 known species of *Potadoma*, and is characterized by a relatively thin shell, with sculpture either absent or, if present, taking the form of two to

<sup>1</sup> Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.



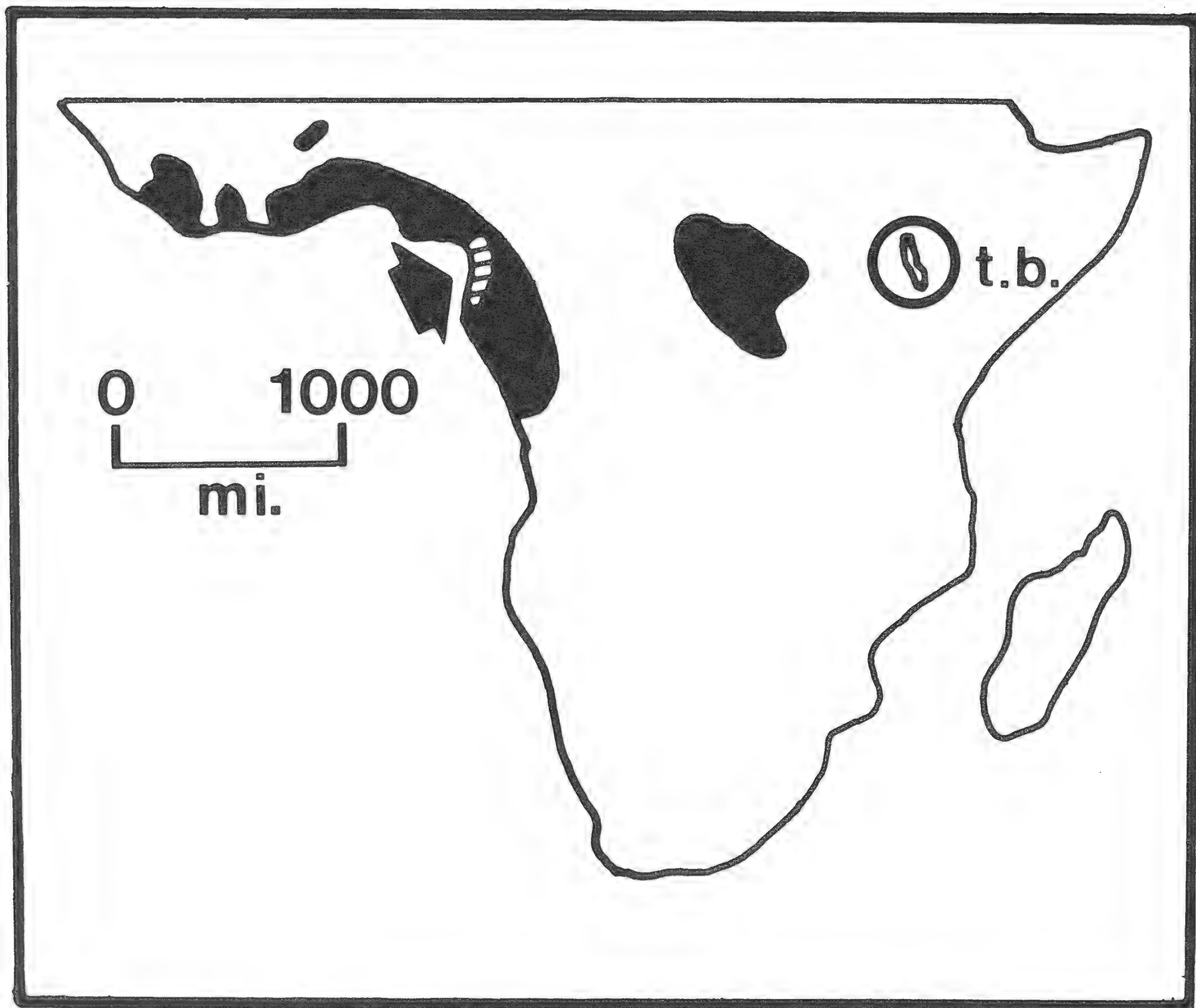


Fig. 1. Present distribution of *Potadoma* in Africa (dark and hatched areas). Circle indicates the Turkana Basin in East Africa, from the western portion of which *Potadoma lomekwiensis* sp. nov., described here, was collected. Hatched area (black arrow) indicates the distribution of the "Camerounian group" of *Potadoma* (*P. zenkeri*, *P. nyongensis*, *P. trochiformis*, and *P. angulata*), the extant forms apparently most closely related to *P. lomekwiensis*.

many spiral carinations extending over the entire whorl (e.g. *P. buttikoferi* (Schepman)). A second, smaller group, involving at most four species and restricted to a small area of Cameroun (see Fig. 1) is characterized by a heavy shell, by the fact that the principal spiral sculpture, if present, is limited to a single strong angulation or keel, and by the marked elongation of the lower part or the aperture (as in *P. trochiformis* Clench) which may even become spout-like (as in *P. nyongensis* Spence). As indicated by the description of the Turkana *Potadoma* material given below, and by Fig. 2, the heavy shell, single main spiral sculptural element and the spout-like extension of the aperture of the Turkana material clearly indicates its affinities with the endemic group of Camerounian *Potadoma* species, at present limited to a restricted area some 1800 miles to the west of the Turkana Basin.

The only fossil example of *Potadoma* hitherto described is *P. ganahli* from the Plio-Pleistocene Kaiso deposits of the Albert-Edward basin (Connolly 1939). The specimen of *P. ganahli* illustrated by Adam (1959) is worn, lacks a strong peripheral angulation and has no abapical extension of the aperture; it is therefore quite unlike *P. lomekwiensis*. Both Adam (1959) and Gautier (1970) refer *P. ganahli* to *Viviparus worthingtoni* (Charig). Better

preserved specimens of this latter species, illustrated by Gautier (1970), have some resemblance to *P. lomekwiensis*, particularly in their pronounced subsutural shoulder and occasional development of a subsidiary carina. But illustrated specimens clearly lack the pronounced abapical extension of *P. lomekwiensis*, and *V. Worthingtoni* is usually considerably larger, although having fewer whorls as an adult (4–5 whorls in adult *V. worthingtoni* as opposed to 6–7 in *P. lomekwiensis*). Certain other endemic viviparids of the Kaiso sequence also bear some resemblance to *P. lomekwiensis* and other extant *Potadoma* species in their development of a pronounced subsutural shoulder, notably *V. nodulosus* (Fuchs) (see Gautier 1970, Pl. II) and *Viviparus? lepersonnei* (see Gautier 1970, Fig. 6). But all lack the pronounced abapical extension of *P. lomekwiensis*, and have fewer whorls. It is indeed possible that some of the Kaiso viviparid species are in fact referable to *Potadoma*; interestingly, Adam (1959) has suggested that the form *Viviparus? lepersonnei* Gautier, which is extremely small for a viviparid, might be referable to the Melaniidae, thereby possibly implicating *Potadoma*, although Gautier rejects this suggestion on the basis of the form of the growth-lines in *V.? lepersonnei* (Gautier 1970, p. 97).

Given the fact that the disjunct distribution of modern *Potadoma* clearly suggests a comparatively recent range-reduction, it would not be surprising if certain of the endemic Kaiso viviparids were in fact referable to *Potadoma*, though as indicated above, the evidence is doubtful. It is noteworthy in this connection that extant *Potadoma* species are restricted to fluviatile situations, whereas the Kaiso faunas appear to occur in exclusively lacustrine settings.

Interesting parallels can be drawn between the late Cenozoic distribution of *Potadoma* and the distribution of another taxon now limited to west and central Africa, the unusual taxodont mutelid genus *Pleiodon* (Conrad). The latter is currently represented in Lake Tanganyika by the relict form *Pleiodon spekei*, but its other representatives are currently limited to western and west-central Africa (Paine and Woodward 1964). However, in the late Cenozoic *Pleiodon* was widely distributed in the western rift (Gautier 1970), in the Lake Victoria region (Verdcourt 1963), and is a prominent element of late Cenozoic faunas of Lake Turkana and the Omo valley to the north (e.g. Williamson 1981, Van Damme 1979). The comparatively recent disappearance of both *Potadoma* and *Pleiodon* from eastern Africa may be attributable to the disruption of direct hydrographic connections between the latter area and west and central Africa concomitant on late Cenozoic rifting activity (Beadle 1979). In the absence of direct hydrographic connection between east and west/central Africa, local extinctions of these forms in the east, a likely consequence of the periodic periods of lake low-stand and enhanced alkalinity known to characterize the late Cenozoic of this area (Beadle 1979) would not be followed by reimmigration from the west, perhaps resulting in the gradual disappearance of both *Potadoma* and *Pleiodon* from eastern Africa.

A final point concerning this intriguing record of *Potadoma* from the western Turkana Basin is that it may provide useful information regarding the paleoecological setting of the important late Cenozoic hominid-bearing beds of the area (Leakey & Leakey 1978): modern species of *Potadoma* are universally restricted to rivers and streams in the rain-forest belt.

#### DESCRIPTION

***Potadoma lomekwiensis* sp. nov.** (Pl. 13).

*Material*: A total of 45 intact specimens from late Cenozoic deposits at two localities in the Lomekwi drainage area, western Turkana Basin (Brown's Salt Lake University collection site numbers 82–735 and 82–736). Stratigraphically, the fauna at site 82–735, the type locality, occurs some 2 m above the fauna at site 82–736; both faunas occur within a few meters of the 'Tulu Bor Tuff' (Brown and Cerling 1982).

*Description:* Shell heavy, high-spired, with the umbilicus partly closed by an extension of the columellar margin. Aperture elongated into a pronounced abapical spout. Sculpture consists of a pronounced adapical keel or shoulder most pronounced on later whorls; subsidiary minor spiral elements may occur abapical to this major keel. Specimens of *Potadoma lomekwiensis* are frequently decollate, as is often the case in this genus.

*Holotype:* Specimen KNMI-WT 15609 in the malacological collections of the National Museums of Nairobi, Kenya.

*Paratypes:* Ten specimens from the type locality, five in the collections of the National Museums of Nairobi (KNMI-WT) and five in the collections of the Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University (MCZ 29184–29188).

Additional material from site 82–736 is in 15610–15614 and in the Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University (MCZ 29189).

*Type Locality:* Brown's (Salt Lake University) collecting site 82–735 in the area of the Lomekwi drainage, western Turkana Basin.

*Potadoma lomekwiensis* is named for the Lomekwi drainage in the western Turkana Basin, the only locality from which it is presently known.

*Measurements:* Height of holotype: 24 mm, width of holotype: 12 mm.

*Remarks:* Overall shell shape, form of aperture and sculptural details seem rather variable in *P. lomekwiensis*, as is commonly the case in certain other members of the genus, notably *Potadoma ponthiervillensis* (Dupuis and Putzeys) and *P. liricincta* (Smith) (Mandahl-Barth 1967, Brown 1980). The modern forms closest to *P. lomekwiensis* seem to the Camerounian species *Potadoma zenkeri* (Martens), *P. angulata* (Thiele), *P. nyongensis* (Spence), and *P. trochiformis* (Clench) from Cameroun. *P. zenkeri* differs from *P. lomekwiensis* in general shell form, in its lack of a keel, and in the fact that its apertural extension is directed adaxially, rather than abaxially, as in *P. lomekwiensis*. *P. lomekwiensis* resembles *P. angulata* in general shell form, but the main keel in the latter occupies an abapical rather than adapical position on each whorl, and the aperture does not show the striking spout-like extension of *P. lomekwiensis*. *P. lomekwiensis* resembles *P. nyongensis* in general form of aperture, but the keel in the latter form is positioned midway on the whorl, rather than adaptically as in *P. lomekwiensis*, and there are differences in general shell form between these two species. *P. angulata* differs from *P. lomekwiensis* in that its principal keel occupies a mid-whorl position, in its low-spired, trochiform shell, and in its lack of an apertural extension. *Potadoma lomekwiensis* appears closely allied to, but is clearly distinct from these four Camerounian species.

#### ACKNOWLEDGEMENTS

Thanks are due to Dr. F. H. Brown, who collected this material, Dr. D. S. Brown, for his helpful comments, and Mr. R. Eng, who took the photographs.

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# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## REPORT OF THE COUNCIL 1984–1985

It is with regret that the Society has to report the deaths of the following 6 members; Mr. A. P. H. Oliver who joined in 1966; Mr. E. Ing who joined in 1963; Prof. Stillman Berry who was a life member who joined in 1946; Dr. L. Gasull who joined in 1977; Mr. R. F. Cumberland and Mr. Drake who were both family members and who both joined in 1963.

The total membership of the Society now stands at 598 and is comprised of the following categories:– Full members 447, Institutional members 37, Full life members 34, Family life members 6, Honorary members 5, Junior members 22, Family members 47.

*Resignations:* Institutional member 1, Full members 23, Family members 2, Total 26.

*Struck-off for non-payment of subscription:* Institutional member 1, Full members 19, Family members 4, Junior members 5, Total 29.

*New members nominated and elected during 1984/5:* Full members 28, Family members 4, Junior members 4, Total 36.

### *Meetings*

There were 7 ordinary meetings held in the Demonstration Room of the British Museum (Natural History), together with one Annual General Meeting. The November Ordinary meeting was a joint meeting with the Malacological Society, the subject being Bivalves.

### *Publications*

Two parts of the Journal of Conchology were issued (Volume 31, parts 5 & 6). Four issues of the Conchologists' Newsletter were printed and issued with the Annual Programme card of events. A full membership list was issued in June. No papers for students were issued.

### *Subscribers*

The total number of subscribers is 155 who took out a total of 169 subscriptions. There were 12 subscribers to the Conchologists Newsletter and Papers for students.

### *Field Meetings 1984*

Two field meetings were held during 1984. Sunday 24th June a joint meeting with the Northampton N.H.S. Saturday 15th. Sept. ancient woodland habitats in northwest Leicestershire. Thanks are due to Mr. A. G. H. Osborn and Mr. J. Mathias for leading these meetings.

## TREASURER'S REPORT, 1984

The accounts for the year show a surplus of £1,364.89.

Expenses were very similar to those for the previous year, with the additional expense incurred by the publication of the Members' List.

The £700 13% borough of Bury Loan came to the end of its term, and was renewed at 9 $\frac{3}{4}$ %.

It is regrettable that there has been a substantial fall in the income from Members' Subscriptions and Entry Fees. Besides a drop in new Members an unusually large number of existing Members failed, despite reminders, to pay the 1984 Annual Subscription; these included 38 Ordinary Members, 2 Institutional Members, 2 Family Members and 5 Junior Members. Members are reminded that no further publications can be sent to those whose current Annual Subscriptions remain unpaid.

Covenanted Subscriptions produced the welcome additional income of £258.03, and the Society is also grateful for the anonymous donation of £100.

Your Council is very concerned regarding the possible imposition of V.A.T. on the Society's publications. Should this occur it may be necessary to call for alterations in subscription rates.

MARJORIE FOGAN  
(Hon. Treasurer)

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND  
INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1984

[illegible]





## PROCEEDINGS

### RECORDER'S REPORT: MARINE MOLLUSCA

Among recent reports, the following are the more interesting records:

*Eulimella nitidissima* (Montagu) is recorded living from Orkney (S3) in 1984 by A. Simpson of the Orkney Marine Biology Unit (Dundee Univ.), the first live post-1950 record in the British area. *Tritonia manicata* Deshayes was found in Jersey (S17) in 1983, by J. G. James, the second British record.

*Doto hystrix* Picton and Brown, a new species described by Picton and Brown from the Scillies (S19) and Co. Cork (S37) in 1980, has now been found in Argyll (S29) and Wexford (S39).

*Onchidella celtica* (Forbes and Hanley). Confirmation of an old West Scotland record of this otherwise strictly south-western species is given by a specimen from Argyll (S29) reported in 1985 by Dr Shelagh Smith.

Confusion is being caused over two pairs of sea-slugs: *Eubranchus doriae* and *E. cingulatus*, and *Palio dubia* and *P. nothus*. Wilson and Picton in 1983 showed that many records of *E. cingulatus* were probably, in fact, of *E. doriae*, and records of these two species should be treated with caution until confirmed (Picton, B. E. (1981), *Ir. Nat. J.* **20** pp. 261–308, Wilson, K. and Picton, B. E. (1983), *Ir. Nat. J.* **21** pp. 69–72). Fortunately, the recent publication of the second volume of the Ray Society opisthobranch monograph, by Thompson and Brown (Thompson, T. E. and Brown, G. H. (1984) *Biology of Opisthobranch Molluscs, vol. II*, Ray Society, London), brings together in convenient and accessible form, descriptions and illustrations of all the nudibranchs, and clarifies the position over these two eubranchids; it also discusses the difference between the two *Palio* species where, again, confirmation of records would be desirable.

Area Representative changes in West Ireland; David McGrath of University College, Galway, is handing over S35 (Mayo) and S37 (Fastnet) to Bernard Picton of Ulster Museum, Belfast, who already looks after S33 (North Donegal). David McGrath is retaining S36 (Galway), and I am grateful to him for the work he has done in Mayo and Fastnet.

D. R. SEAWARD

### RECORDER'S REPORT: NON-MARINE MOLLUSCA

#### A. Grid mapping

Excellent progress was made during 1984 in mapping poorly known areas of the British Isles. Especially noteworthy is the systematic work of Mr A. O. Chater in Cardiganshire, and of a Conchological Society field party in southern Ireland (Mrs M. Fogan, Mrs E. B. Rands and Dr A. J. Rundle).

Plans are well advanced for the long-promised new edition of the *Atlas*, though it seems unlikely that this will go to press before the end of 1985. An attempt is being made to extract systematically old published records in order to illustrate distribution changes of the past century as clearly as possible.

#### B. Vice-comital records

The following new records have been verified since the last Report (*J. Conch., Lond.* **31** p. 386). Unless stated otherwise, all date from 1984–5. The Irish records were made during the mapping expedition in September 1984 (see above).

Sussex West (13): *Phenacolimax major*, Lodsworth (41/9323), A. O. Chater.

Kent West (16): *Arion fasciatus*, *Phenacolimax major*, Ightham Common (51/5754), A. J. Rundle and E. G. Philp.

Surrey (17): *Arion 'lusitanicus'* (Quick's form), Addington (51/3563), Miss S. M. Davies.

Essex South (18): *Pseudamnicola confusa*, Barking Creek (51/4483), G. Harris.

Suffolk West (26): *Boettgerilla pallens*, Ickworth Park (52/8161), I. J. Killeen.

Norfolk West (28): *Anisus vorticulus*, Little Ouse, Hockwold cum Wilton (52/7286; dead shell), Mrs E. B. Rands, 1980; *Helicigona lapicida*, West Acre (53/7815), D. Guntrip.

Hereford (36): *Lymnaea glabra*, Brilley (32/2751), K. Alexander.

Worcester (37): *Milax gagates*, West Malvern (32/7646), P. F. Whitehead.

Cardigan (46): *Acicula fusca*, Glaspwll (22/7397); *Vertigo lilljeborgi*, Tyhir, Llangybi (22/6152); *Arion 'lusitanicus'* (Quick's form), Llangeitho (22/5959); *Trichia plebeia* Pwllcarrel (22/3642), all A. O. Chater.

Leicester (55): *Acicula fusca*, Groby (43/5208), D. T. Holyoak.

Nottingham (56): *Limax tenellus*, Clumber Park (43/6273), K. Alexander.

Chester (58): *Gyraulus laevis*, Church Coppenhall (33/7158), K. G. Allenby.

Isle of Man (71): *Arion 'lusitanicus'* (Quick's form), Douglas (24/3877), Miss S. M. Davies.

Peebles (78): *Deroceras agreste*, West Linton (36/1353), A. T. Sumner.

Perth East (89): *Pupilla muscorum*, Kinnoull Hill (37/1322), Mrs D. K. Marriott.

Aberdeen South (92): *Zonitoides nitidus*, Loch Kinnord (37/4499); *Milax budapestensis*, Aberdeen (38/9109), both Mrs D. K. Marriott.

Banff (94): *Ceruella virgata*, Findochty (38/4668), A. O. Chater.

Cork West (H3): *Vallonia costata*, Timoleague (10/4743); *Boettgerilla pallens*, *Limax maculatus*, Ballinadee (10/5651); *Cecilioides acicula*, Clonakilty (10/3940).

Cork Mid (H4): *Ovatella myosotis*, Ballinclashet (10/6951); *Arion fasciatus*, *A. owenii*, *Zenobiella subrufescens*, *Arianta arbustorum*, Mount Rivers (10/7361); *Boettgerilla pallens*, Ovens Bridge (10/5469).

Cork East (H5): *Limax cinereoniger*, Ross River Woods (10/6396); *Limax flavus*, Rostellan (10/8665).

Waterford (H6): *Milax gagates*, *Ashfordia granulata*, Bunmahon (20/4398); *Boettgerilla pallens*, Dungarvan (20/2492).

Kildare (H19): *Arion lusitanicus* seg., Old Kilcullen (22/8207); *Arion fasciatus*, Kilrush Lodge (22/7803).

Some of the more interesting of the new vice-comital records are as follows:

*Pseudamnicola confusa*. In the mid-19th century *P. confusa* was abundant in marshes along the lower Thames between Greenwich and Tilbury. It was believed extinct in the Thames estuary by 1900 through industrial pollution. The discovery of a small colony in a tidal marsh on the Essex side is therefore a considerable surprise. A full account will be found on p. 147 below.

*Lymnaea glabra*. During the past century this snail has disappeared from many areas as a result of the destruction of ponds on lowland heaths and commons by arable farming. The new site in Herefordshire (two closely adjacent swampy ponds in rough pasture) is the only locality now known to exist in the Welsh Borders.

(*Lymnaea stagnalis*. The record from v.c. 46 published in last year's Report (pool in dunes at Ynyslas; 22/6194) has turned out to be based on a deliberate introduction made in 1980.)

*Anisus vorticulus*. A single half-grown bleached shell of uncertain age was recovered from flood rubbish of the Little Ouse. This rare mollusc has not been found living nearer than the Norfolk Broads, though a dead shell is recorded at Redgrave Fen in the Waveney valley about twenty miles east of the present site (*J. Conch.*, Lond. **12** (1909) p. 280) and Postglacial fossils are known from Cambridgeshire. It is of interest that fresh shells of the equally rare *Valvata macrostoma* were present in the same sample from Hockwold, confirming a record from here made in 1926.

*Vertigo lilljeborgi*. The new site in Cardiganshire is the second known in Wales and the most southerly in Britain. This colony is almost certainly a relict from the end of the glacial period. The swampy hollow in which it occurs appears to be a kettle hole (see p. 147, below).

*Arion owenii* (= *A. hortensis* 'form B'). Not hitherto reported from southern Ireland (Cork Mid; one site only) and representing a great extension in the known range of the species. The two much commoner segregates of the *Arion hortensis* complex (*A. hortensis* seg., *A. distinctus*) were detected in 1984 in five southern Irish vice-counties (Cork West, Cork Mid, Cork East, Waterford, Kildare), the former species being much the more frequent.

*Boettgerilla pallens*. Probably a recent arrival in southern Ireland. The new sites in Cork and Waterford are on roadsides and waste ground, usually associated with *Milax budapestensis* and *Deroceras caruanae*.

*Limax tenellus*. The presence of this slug in oak/beech woodland at Clumber is a useful indicator of the essentially ancient, primary nature of this fragment of Sherwood Forest.

*Arianta arbustorum*. A species hitherto regarded as restricted to the north in Ireland and unexpected in Co. Cork. The two roadside sites in Cork Mid are in relatively rough, semi-wild country harbouring *Acicula fusca* and *Zonobiella subrufescens*. Old records from 'Killarney' (1840) and from 'near Limerick' (1887) now seem less improbable.

*Helicigona lapicida*. This species is now something of a rarity in eastern England (where there are many 19th century records, though surprisingly none for Norfolk West). At West Acre it was found alive in a wooded chalk pit.

M. P. KERNEY



## COMMUNICATIONS

### INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

ITZN 59

The following Opinions have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature*, volume 42, part 1, on 2 April, 1985:

*Opinion No*

1292 (p. 27) *Voluta papilio* Link, 1807 (Gastropoda): conserved.

1296 (p. 37) Request for the use of the plenary powers to conserve *Nettastomella* Carpenter, 1865 (Bivalvia) refused.

(p. 43) Correction of Entry No. 462 in the Official List of Generic Names in Zoology concerning *Sphaerium* Scopoli, 1777 (Mollusca, Bivalvia) (Correction to Opinion 94).

ITZN 11/5 A.N.(S.) 133

The Commission hereby gives six months notice of the possible use of its plenary powers in the following cases, published in the *Bulletin of Zoological Nomenclature*, volume 42, part 1, on 2 April, 1985 and would value comments and advice on them from interested zoologists.

*Case No.*

2340 *Spiroglyphus* Daudin, 1800 and *Stoa* De Serres, 1855 (Mollusca, Gastropoda, Vermetidae): proposed suppression of two equivocal generic names.

2331 Homonymy in the families HARPIDAE Hawle & Corda, 1847 (Trilobita) and HARPIDAE Bronn, 1849 (Mollusca, Gastropoda).

P. K. TUBBS, Executive Secretary, ICZN  
c/o British Museum (Natural History), Cromwell Road, London, SW7 5BD  
(Received, 2 April 1985)

### *VERTIGO ALPESTRIS* & *VERTIGO SUBSTRIATA* IN FRANCE

This communication describes three new records for *Vertigo alpestris* Alder, 1838, six new records for *Vertigo substriata* (Jeffreys, 1833) and adds some notes for these and other Vertiginidae in France.

Bas-Rhin; La Cascade du Nideck, 20 km SSW. of Saverne: LU 78, 1.9.79. 1) Ivy-covered rock face; dead shells of both *V. alpestris* and *V. substriata* sifted from leaf litter. 2) Stream above cascade; *V. substriata* amongst *Chrysosplenium oppositifolium* L., with *Columella edentula* and *Bythinella dunkeri*.

Bas-Rhin; N. end of Etang la Fosse near Tieffenbach, 18 km NNW. of Saverne: LV 76, 3.9.77. *V. substriata* and *V. antivertigo* alive under moss under *Urtica dioica* L.

Hautes Pyrénées; W. of Col du Soulor, 22 km SW. of Lourdes: YN 25, 11.7.81. *V. substriata* abundant with *V. antivertigo*, amongst *Juncus* sp., *Carex* sp. and *Menyanthes trifoliata* L.

Cantal; Salers. 1) Anglards de Salers, 9 km NNW. of Salers, opposite Chateau de la Tremoulière: DL 60, 15.7.84. *V. alpestris* among leaf litter on old overgrown wall and under some climbing plants. 2) Chateau de Palemont, 2 km SW. of Salers: DK 96, 15.7.84. *V. alpestris* on ivy-covered wall of chateau.

Puy-de-Dôme; Le Mont Dore. 1) Col de la Crois St. Robert, 3 km WSW. of Le Mont Dore: DL 85, 10.7.84. *V. substriata* on flushed roadside verge with *Juncus* sp., *Carex* sp. *M. trifoliata*, *C. oppositifolium* and *Sphagnum* sp.

2) Near Lac de Guéry, 5 km N. of Le Mont Dore: DL 86, 11.7.84. *V. substriata* with *Juncus* sp., *Carex* sp., *M. trifoliata* and *Salix* sp.

Hte.-Loire; 15 km. SW. of Le Puy, between St. Jean-Lachalm and Cayres: EK 67, 17.7.84. *V. substriata*, *V. antivertigo* and *V. pygmaea* all abundant, with *Punctum pygmaeum*, *Lymnaea truncatula*, *Carychium minimum*, *Cochlicopa lubrica*, *Nesovitrea hammonis*, *Deroceras laeve*, *Euconulus alderi*, in flushed area with *Juncus* sp., *Carex* sp., *M. trifoliata*, *Filipendula ulmaria* L., *C. oppositifolium* and *Orchis* sp.

Loir-et-Cher; between Chambord and Thoury, 4 km ENE. from Chambord in National Reserve de Chasse: CN 97, 19.7.84. *V. moulinsiana* and *V. antivertigo* under *Carex* sp. and *Glyceria maxima* Hartman in an open area of forest.

Judging from the published records of *Vertigo substriata* and *V. alpestris*, both species would appear to be rare in France. Several localities for *V. substriata* are quoted by Germain (*Faune de France* **21** (1930) p. 444) and there is a more recent record from Pyrénées Orientales (*Basteria* **48** (1984) pp. 1070–1071). *V. alpestris* was formerly known in France only from shells found in debris of the Rhône, N. of Lyons (*Faune de France* **21** (1930) p. 447). The notes given above are the results of opportunistic collection not those of a systematic search, and therefore it is probable that both *Vertigo* species and particularly *V. substriata* are more widespread in France than was previously believed.

B. COLVILLE  
26 North Parade, Leeds  
(Received, 18 February 1985)

## GULELLA CONICODENTATA RECORDED FROM KENYA

Amongst a miscellaneous East African collection lent to me by Dr. Martin Pickford of the National Museum, Nairobi, Kenya was a single specimen of *Gulella conicodentata* K. L. Pfeiffer (Streptaxidae), previously known only from two specimens, the holotype and a paratype, collected under stones in 'Steppe' between Moshi and Arusha in N. Tanzania by K. L. Pfeiffer and described by him (*Arch. Moll.* **81** (1952) p. 95, Pl. 2, Fig. 11). Pickford's specimen was collected on 31 Oct. 1982 at the Makindu Limeworks about 165 km. SE. of Nairobi and about 145 km. NE. of the road between Moshi and Arusha and presumably in rather more wooded country. Reassuringly the single shell keyed easily to *conicodentata* in my own keys to the East African species (*Ann. Mus. Roy. Afr. Centr., Sci. Zool.* **8**° (1962) n. 106). I am indebted to Dr. Ronald Janssen of the Senckenberg Museum, Frankfurt for comparing the specimen with the holotype and reporting 'that it perfectly agrees'.

B. VERDCOURT  
Spring Cottage, Kimbers Lane, Maidenhead, Berks. SL6 2QP  
(Received, 22 February 1985)

## BULIMUS OVOIDEUS BRUGUIÈRE 1789 A NAME USED FOR TWO QUITE DIFFERENT SNAILS

At a meeting of the Conchological Society in 1984 Dr. E. Sándor exhibited a characteristically perfect selection of Philippine Islands *Helicostyla*. Whilst he was giving his explanation of this exhibit my attention was immediately drawn when he mentioned the genus *Canistrum* with a species *C. ovoideum* based on *Bulimus ovoideus* Bruguière (*Encycl. Méth., Vers* **1** (1789) p. 335). Now to any old East African hand like myself this is the original name of a very well-known large streptaxid *Edentulina ovoidea* (Brug.) which I used to watch eating slugs very much larger than itself at Amani in Tanzania. At the meeting Dr. Sándor assured me that he had checked the reference thoroughly and looked at the drawing in Lister which Bruguière cited (*Historiae sive synopsis methodicae Conchyliorum* (1685) Pl. 13, Fig. 8). This is the only instance I know of where the same name has been the basis of two names for absolutely different species—*Canistrum ovoideum* (Bruguière) (Fruticicolidae: Helicostyliinae) and *Edentulina ovoidea* (Bruguière) (Streptaxidae). Several of the standard works use these two names without realising the duplication (e.g., Tryon & Pilsbry, *Manual of Conchology* **1** (1885) p. 82 and **8** (1892) p. 43; Thiele, *Handbuch der Systematischen Weichtierkunde* **2** (1931) p. 691, 730, Zilch, *Handbuch der Paläozoologie*, **6** Gastropoda, teil 2 Euthyneura (1960) pp. 563, 635). More popular writers also repeated the error (e.g., Webb, *Foreign Land Shells* (1948) Pl. 25, Fig. 1 & Pl. 131, Fig 8).

I communicated my findings to Dr. Sándor and he rechecked. Bruguière's name can of course only be used for one species; the problem is to determine which one. Bruguière gives quite a detailed description in French and although he cites the Lister figure he points out that his specimen differs in having no black sutural band, a slit-like umbilicus and a fine subsutural spiral groove. It was not at all an uncommon practice in the 18th century and even later for an author to cite a pre-Linnaean reference and/or figure which he *thought was identical* with the species he was describing but which later research proved to be different. In this case the syntype derived from the literature must be set aside and the specimen actually described chosen as the lectotype. Unfortunately, although Bruguière's collection was acquired by the Paris Museum in 1799 the material was relabelled by Lamarck and only very few specimens can now be certainly identified. Dr. Simon Tillier kindly informed me that no trace of Bruguière's specimens of *Bulimus ovoideus* can now be found but there is no doubt as to their identity. The epithet has to be reserved for the streptaxid, *Edentulina ovoidea*. The correct name for the Philippine species is *Canistrum luzonicum* (Sowerby) based on *Bulimus luzonicus* Sowerby 1833.

## COMMUNICATIONS

Dr. Sándor suspects that the error began with Pilsbry in Tryon (*Man. Conch.* **8** (1892) p. 43 where he wrongly referred Bruguière's species to *Canistrum*. In his defence it must be said that he dealt with tens of thousands of species and made few mistakes of this gravity. It is indeed strange that this dual use has gone on for so long, even though, as Sándor has said (*in litt.*), 'there are few people who have been expert on both African and Philippine land shells'. Pilsbry himself did not get involved with African collections in detail until some years later. If anyone has already commented on this confusion then his remarks have been forgotten and overlooked by the great compilers. It is fortuitous that I happened to be at the meeting else the duplicity would probably have lasted a good deal longer.

BERNARD VERDCOURT  
Spring Cottage, Kimbers Lane, Maidenhead, Berks. SL6 2QP  
(Received, 22 February 1985)

### *PSEUDAMNICOLA CONFUSA* REDISCOVERED IN THE THAMES ESTUARY

The hydrobiid *Pseudamnicola confusa* (Frauenfeld) formerly occurred in large numbers on sedge and rush-covered mud banks along the southern (Kentish) bank of the Thames (Reeve, *The Land and freshwater mollusks indigenous to, or naturalized in, the British Isles*. London (1863); Tate, *Science Gossip* **8** (1872) pp. 265–268) and at Tilbury, Essex (Marshall, *J. Conch., Lond.* **6** (1889) p. 141. The species declined rather dramatically towards the end of the nineteenth century and was believed to be extinct in the London area by 1899 (see review by Castell, *J. Conch., Lond.* **25** (1962) pp. 97–117).

On 3 July 1984, along with other members of the Passmore Edwards Museum Biological Survey Team, I visited a reed bed at Cuckold's Haven which is situated two miles from the Thames on the River Roding (TQ 441831). Living on the mud sheltered by reeds were numerous molluscs, including *Potamopyrgus jenkinsi* (Smith), *Lymnaea truncatula* (Müller) and large numbers of *Assiminea grayana* Fleming. Two specimens of *P. confusa* were also found. The surrounding vegetation growing on the mud consisted mainly of *Phragmites australis* (Cav.) Trin. ex Steudel, with smaller numbers of *Aster tripolium* L., *Atriplex prostrata* Boucher ex DC, *Rumex crispus* L. and *Iris pseudacorus* L. Subsequent visits were made in November, during one of which a further 6 specimens were found. From these visits it became apparent that *P. confusa* is locally distributed within the reedbed, presumably reflecting the limited habitat preferences of the species (mud shaded by vegetation and occasionally covered by tidal water of low salinity.). Further visits are planned during which it is hoped that a more precise picture of the distribution of *P. confusa* at Cuckold's Haven can be built up.

The identification of a new locality for *P. confusa* is of national importance. The species appears never to have been abundant in Britain and is restricted, with the exception of a single old record from the Bristol Channel, to the east and south-east. Since 1950 it has been found only in six 10-kilometre squares (Kerney, *Atlas of the non-marine Mollusca of the British Isles*. Huntingdon (1976)). In common with many estuarine sites all six are threatened by environmental changes which would certainly conflict with the habitat requirements of *P. confusa*.

I should like to thank Miss S. J. Lambert for identifying the vegetation growing on the mud, and Mr. F. Naggs and Dr. M. P. Kerney for confirming the identification of *P. confusa*.

GERARD J. HARRIS  
Passmore Edwards Museum, Romford Road, Stratford, London E15 4LZ  
(Received, 20th February 1985)

### *VERTIGO LILLJEBORGI* LIVING IN CARDIGANSHIRE

The late glacial relict *Vertigo lilljeborgi* (Westerlund) is known from scattered sites in western Ireland, Scotland and the Lake District, and from one site in Snowdonia (Dance, *J. Conch. Lond.* **27** (1972) pp. 387–389). In July and October 1984 I found eight living specimens in a site near Llangybi in Cardiganshire (V.C. 46), extending its range southwards in Britain by some 90 km. The site (SN610529) is a roughly circular depression *ca* 100 m across in a wide terrace at the base of the south-east slope of the valley of the Afon Dulas at an altitude of 135 m. D. Q. Bowen (*pers. comm.*) has identified this depression as a large kettle hole, the result of the melting of glacial ice lenses trapped in the fluvio-glacial sands and gravels which accumulated in this valley towards the close of the Late Devensian glaciation. The depression thus dates from about 15,000–13,000 B.P. A railway embankment, built in the 1860s and now disused, cuts across the south-east edge of the depression.

The steep pasture slope encircling the depression is sharply delimited from the apparently largely floating mass of poor fen vegetation that fills the bottom, and the whole fen is normally so wet that only the marginal zone of it is grazed. This marginal zone is 7–10 m wide and dominated by *Juncus effusus* L. and the moss *Calliargon*



*giganteum* (Schimp.) Kindb., with locally abundant *Carex curta* Good., *Potentilla palustris* (L.) Scop. and *Menyanthes trifoliata* L. There is a good deal of standing water in wet seasons. One specimen of *V. lilljeborgi* was found here by searching litter and moss collected from the base of *Juncus effusus* tussocks, as well as a few *Euconulus alderi*, *Deroceras leave* and *Nesovitrea hammonis*. In from this is a zone ca 10 m wide, usually without any standing water, dominated by *Sphagnum fimbriatum* Wils., *S. recurvum* P. Beauv. and *S. subnitens* Russ. & Warnst., with locally abundant *Juncus acutiflorus* Hoffm., *Hydrocotyle vulgaris* L. and the moss *Aulacomnium palustre*. The only molluscs found in this *Sphagnum* zone were *Euconulus alderi* and *Nesovitrea hammonis*. The centre of the fen is dense scrub of *Salix cinerea* L. with bushes 4–5 m high and much standing water. *Carex nigra* (L.) Reich. and *Sphagnum squarrosum* Crome are the dominants, *Menyanthes trifoliata*, *Potentilla palustris* and *Valeriana officinalis* L. are locally frequent, and there are a very few plants of *Juncus acutiflorus* and tussocks of *Molinia caerulea* (L.) Moench. The mosses *Calliergon giganteum* and *C. cuspidatum* (Hedw.) Kindb. are dominant on and around the bases of the *Salix* trunks and in moss and leaf litter collected from the bases of these trunks seven specimens of *V. lilljeborgi* were found, along with abundant *Euconulus alderi*, *Carychium minimum*, *Nesovitrea hammonis* and *Punctum pygmaeum*.

Although there is no inflow stream, the depression is notable for its tendency to flood after heavy rain. The largely artificial outflow channel to the north-west is cleared out at intervals to prevent this. *V. lilljeborgi* is known to be characteristic of sites subject to flooding (Kevan & Kerney, *J. Conch. Lond.* **19** (1933) pp. 296–313; Kerney, *J. Conch. Lond.*, **28** (1974) p. 228). I have searched the only kettle hole lake in Cardiganshire, Maes-Llyn, and a number of pingos in the Cledlyn and Clettwr valleys further west in the county that provide somewhat similar habitats, but none of these sites flood to the same extent either because of different topography or because of more efficient drainage, and the only *Vertigo* species they appear to contain are *V. antivertigo* and *V. substriata*.

I am grateful to Dr. M. P. Kerney for identifying the *V. lilljeborgi* specimens, to Professor D. Q. Bowen for revisiting the site and confirming his ideas on its origin, to Mr. A. Eddy for identifying the mosses, and to Mr. B. R. Osborne, Ty-hir, Llangybi for permission to visit the site.

A. O. CHATER

Windover, Penyrangor, Aberystwyth, Dyfed SY23 1BJ

(Received, 19 April 1985)

## CORRECTIONS AND ADDITIONS TO THE LANDSNAILS OF SOUTHERN LEBANON

Recently the author received the landsnails from southern Lebanon reported on by Heller in 1984 (*J. Conch. Lond.* **31** pp. 331–336) for permanent storage in the mollusc collection of the Hebrew University of Jerusalem (HUJ). A review of the material revealed two errors in the identifications, while a shell of *Monacha obstructa* (Pfeiffer, 1842), a species not mentioned by Heller, was found in a shell of *Helix engaddensis* Bourguignat, 1852 from Tyre. This *Monacha* was also encountered in material received from other sources in southern Lebanon. The following corrections and additions have to be made in Heller's list:

*Oxychilus* (*Schistophallus*) *syriacus* (Kobelt, 1878). Jezzin, 2 km north of the town, leg. J. Heller, December 1982 (HUJ 12024/1). Heller reported this specimen as *Eopolita protensa*. However, its completely smooth shell and some differences in form rule out that identification. In fact the shell fits exactly the description of *Oxychilus syriacus* as given by Riedel 1962 (*Ann. Zool. Warszawa* **20** pp. 275–279). Riedel also discusses the known range of that species.

*Monacha obstructa* (Pfeiffer, 1842). Tyre, leg. J. Heller, December 1982 (HUJ 11986/1); valley of Damur river, about 10 km from the sea, leg. A. Fast, August 1982 (HUJ 11716/2); near Sidon, leg. A. Fast, July 1982 (HUJ 11718/1). This is a common species in the Middle East, where it has been reported often under the name of *Monacha schotti* (Pfeiffer, 1857)—a junior synonym. Usually it is found on the ground, most often under stones, fallen trees and all kinds of debris.

*Metafruticicola berytensis* (Pfeiffer, 1841). Sidon-Jezzin road, above the Awwali River, leg. J. Heller, December 1982 (HUJ 11992/1). This shell was identified by Heller as belonging to *Metafruticicola fourousi* (Bourguignat, 1863). The latter is characterized by a much larger granulation on the shell. This correction of the identification does not mean that *M. fourousi* has to be deleted from the list of landsnails living in southern Lebanon. In the collection we have a sample which was collected near the Litani river on 20 September 1942 (HUJ 32121/2).

Thanks are due to Mr. A. Fast (Kibbutz Netzer Sereni) for collecting landsnails in Lebanon.

HENK K. MIENIS

Zoological Museum, Hebrew University, Jerusalem, Israel

(Received, 19 April 1985)

## REVIEWS

*The Marine Mollusca of the Bay of Algeciras, Spain, with general notes on Mitrella, Marginellidae, and Turridae.* By J. J. Van Aartsen, H. P. M. G. Menkhorst and E. Gittenberger. *Basteria*, Supplement No. 2, 1984, pp. 1–135.

A short and inadequate description of this publication would be that it lists 393 species of Mollusca (out of 629 known from the area) collected by the first two authors from shell-sand from Algeciras Bay, 203 of which had not been recorded there before, and seven of which are described as new species. This in itself would make it a significant addition to our knowledge of the malacofauna of S.W. Iberia, but there is also a wealth of useful supplementary information. Over 220 of the species listed are illustrated, mostly as superb SEM photographs; 208 figures show gastropods and 18 bivalves, the unbalanced split being because the latter appear to present fewer problems. These illustrations, selected to show new or rarely illustrated species, are a major strength of the paper and make it a worthwhile buy for them alone.

Comments are provided on most of the species listed; these are generally very helpful, particularly on distinguishing features, and include relevant references with emphasis on recent illustrations. Some, however, like ‘a common European cockle species’ could have been left out without detriment to the value of the work. There is little indication of approximately how much material of the various species was found.

As a consequence of working shell-sand the new taxa have been described from shells alone (as fossils are) with no data on animals or habitat; this is something of a pity, particularly in the case of *Hydrobia joossei* which is presumably a brackish or freshwater species. Descriptions of the shells of the new taxa are adequate though dimension are given as ranges and the only measurements of types refer to those illustrated. Also, it is not clear what specimen was used to illustrate the new species *Alvania altenai*, *Gibberula janseni* and *Cypraeolina vanhareni*; it would be helpful if the authors could clarify this point for the benefit of later workers on these molluscs.

The general notes are valuable collations of the authors’ literature searches, examinations of types, and conclusions (for example: nomination of a lectotype for *Gibberula recondita* Monterosato, 1884) which would form a useful base for later revisions. They cover *Mitrella* worldwide, east Atlantic and Mediterranean Marginellidae and the *Raphitoma/Philbertia* complex in the Turridae. In the last case the authors’ judgement on the identity of the type species of *Raphitoma* Bellardi, 1847 is sensible and no one is ever likely to get nearer to what the truth was, though whether the protoconch alone is a sufficient character on which to separate turrid genera is questionable despite its being so used in the past.

Minor errors, typographical or otherwise are few indeed. I am grateful to Mr Tom Pain FLS for pointing out that *Phyllonotus trunculus* (page 35) should be *Hexaplex trunculus*; *Phyllonotus* is a New World genus. The new species *Odostomia kromi* is omitted from the abstract.

In sum, this is a valuable publication and thoroughly recommended to all interested in east Atlantic and Mediterranean Mollusca. It is obtainable from the: Nederlandse Malacologische Vereniging, c/o Dr. H. E. Coomans, P.O. Box 20125, NL-1000 HC AMSTERDAM, The Netherlands. The price is Hfl 30 plus Hfl 5 postage, Hfl 35 in all, to be paid in advance either to Post Office Giro 28 80 32, the Hague in the name of ‘Nederlandse Malacologische Vereniging’ or direct by postal order to the Hon. Treasurer of the Society, Dr. A. C. van Bruggen, Terweeweg 1 A, NL-2341 CL Oegstgeest, The Netherlands.

D. C. LONG

*Thesaurus Conchyliorum or monographs of genera of shells. Monograph of the genus Natica by G. B. Sowerby. London, 1883. Reprint 1984 with an analytical check list of Sowerby’s species.* By R. Michael Dixon. 29 pp. 9 coloured plates. L. P. Burnay, Lisbon.

This reprint consists of a folder containing a complete reproduction of Sowerby’s original text and 9 loose plates in a pocket at the back. The check list is not bound up with the text, which makes it much easier to use.

The publisher is to be congratulated on the beautiful reproductions of Sowerby’s original plates, which are in every respect satisfactory. This reprint makes available to all interested an important contribution to the study of the Naticidae since few could aspire to own a copy of the now rare and very costly Thesaurus.

Its value is greatly enhanced by the addition of an analytical check list of Sowerby’s species by one of the worlds leading authorities on the Naticidae, R. Michael Dixon. In this the present taxonomic status of each of the 144 species illustrated is given, making it of real practical use to anyone working on this family.

This publication is undoubtably a must for anyone working on this neglected but fascinating family of marine gastropods and one can only echo the hope expressed by Michael Dixon in his introduction, that the plates will stimulate a wider popular interest in these beautiful, underrated and little studied shells.

Copies can be ordered direct from the publisher Mr. L. P. Burnay. Apartado 1013, 1001 Lisboa, Portugal. Price \$9.00 plus \$2.00 registered post.

T. PAIN

*World-wide Snails. Biogeographical studies on non-marine Mollusca.* Edited by A. Solem and A. C. van Bruggen, ix+289 pp., E. J. Brill/W. Backhuys, Leiden, 1984. Price 85 guilders. ISBN 90 04 074171.

Widespread interest in the biogeography of land and freshwater Mollusca led to a 'Colloquium on Non-marine Mollusc Biogeography' being held at the 8th International Malacological Congress in Budapest, Hungary in 1983. This collected work presents the text of the 19 main papers presented at the Colloquium.

The balance of papers in this book shows how the emphasis of studies in molluscan biogeography has mainly moved on from descriptive to analytical approaches. Thus for example there are studies of colonisation of newly emerging islands by land snails (Valovirta); of species numbers on islands (Cook, Mylonas, Solem); of equilibrium species numbers and the chemistry of lakes (Aho); as well as studies of the effects of climatic history on the faunas of tropical (Verdcourt), arid (Heller) and temperate regions (Grossu).

The role of earth history in explanation of patterns of distribution is submitted to critical analysis on several time scales, ranging from the role of continental drift in explaining inter-continental differences and similarities of faunas (Meier-Brook, Walker) through analyses of details of faunal exchanges at edges of colliding plates and plate fragments (Giusti & Manganelli, Mordan, Waldén), to studies of responses to climatic fluctuations in the Quaternary. Nonetheless, although several authors critically appraise the pertinent palaeontological data, others do not and in some cases there is little fossil evidence to assess so that reconstructions of former patterns of distribution may be viewed as speculative models rather than established fact.

Another trend evident in studies of molluscan biogeography is towards a blurring of traditional distinctions between ecology and biogeography, as these approaches are increasingly often shown to be complementary. In this context the paper presenting 'A world model of land snail diversity and abundance' by Solem is of particular importance in identifying the need for further studies of the interaction of life-history, habitat and longer term geological history in determining the numbers of land snail species found coexisting. It is perhaps remarkable that despite the potential importance of interspecific competition (or the lack of it) in providing restraints on species numbers there have been remarkably few rigorous demonstrations of the extent of competition between natural land snails populations.

Several more traditional zoogeographical studies presented here adopt descriptive approaches and seek patterns of faunal affinity. Thus, van Bruggen and Meredith describe the rapidly increasing knowledge of land snails in Malawi, Szekeres describes the wider affinities as well as patterns of regional endemism of South American Clausiliidae, Smith reviews regional endemism in Australian land snails, and patterns of faunal affinity are discussed for Madeira (Waldén) and Rumania (Grossu). Interpretation of patterns of distribution through inference of faunal history is the main aim of most of these studies. In contrast, André presents studies on the land snail faunas of Mediterranean parts of France and the Iberian Peninsula where the main aim appears to be quantitative measurement and classification (aided by computer) of the extent of similarity in numerous local faunas.

The importance of a sound basis of systematic studies is stressed by several of the authors, and exemplified by Gittenberger's review of distributional history in the Chondrininae or Mordan's for the Enidae of southern Arabia. Other authors comment that inadequate current levels of systematic understanding hinder detailed biogeographical study, as for example with Lymnaeidae.

Overall, this book is to be recommended to biogeographers in general for the wealth of interesting material and different approaches it contains. Differences from the better known studies in vertebrate zoogeography are instructive because of the greater antiquity of many of the molluscan groups and their different dispersive abilities. For malacologists especially interested in land or freshwater molluscs it provides a valuable synthesis in English of material that is otherwise widely scattered, along with several important new contributions. The book is well produced in paperback, with numerous maps and other figures. It is also well indexed.

D. T. HOLYOAK



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Manuscripts should be sent to:— **Dr M. P. Kerney, Department of Geology, Imperial College, London SW7 2BP.**

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# PREHISTORIC UTILIZATION OF TROPICAL REEF MOLLUSCS IN EAST TIMOR INDONESIA

EMILY GLOVER<sup>1</sup>

*(Accepted for publication, 19th October 1985)*

*Abstract:* The analysis of shell samples from archaeological sites in Timor, Indonesia, provides evidence for the long exploitation of Mollusca. Molluscs were collected from the nearby fringing reef and species from estuarine and terrestrial habitats were also recorded. There is some evidence that exploitation of the molluscs may have caused changes in the structure of the local populations, particularly affecting abundance and size range.

## INTRODUCTION

Archaeologists have long been aware of the close relationship between molluscs and man. Some of the earliest evidence comes from cave sites in south-eastern Africa, where mollusc food remains were found from as early as 120,000 years ago (Voigt 1975). This is an unusual situation for sites of this age have not usually survived changes in sea level during the Pleistocene, and the worldwide proliferation of shell middens occurs only from about 8000 years ago when sea levels stabilized close to present heights (Chappell & Thom 1977).

Until the 1950's, when attempts were made to quantify shell midden samples for the first time (Cook & Treganza 1947, 1950) most site reports simply listed species with no record of changes in abundance within or between the levels of a site. However a more ecological approach to archaeological evidence has led to increasing sophistication of methods.

In general archaeologists use mollusc shell samples to provide information on prehistoric subsistence economies, and variations in the relative abundance of particular species have been interpreted in three main ways; as changes in the preference of collectors; as the depletion of species through excessive human predation; and as an indicator of external environmental changes through alteration of species composition in the habitat. In practice it is usually difficult to specify the criteria that will discriminate between various interpretations, for the methods of archaeological sampling and analysis are crude and there is never enough specific knowledge of past environments.

Nevertheless there is a growing amount of archaeological evidence for the long and varied use of molluscs by man and it is perhaps surprising that biologists, who study the present day mollusc populations have so frequently ignored effect of human exploitation upon populations when it is clear that man has been an active predator along much of the world's coastlines for so long. In this paper I examine the archaeology of mollusc utilization at a site in East Timor and hope to show how long term exploitation by man may have affected ancient mollusc populations.

<sup>1</sup> 104 Lofting Road, London N1.

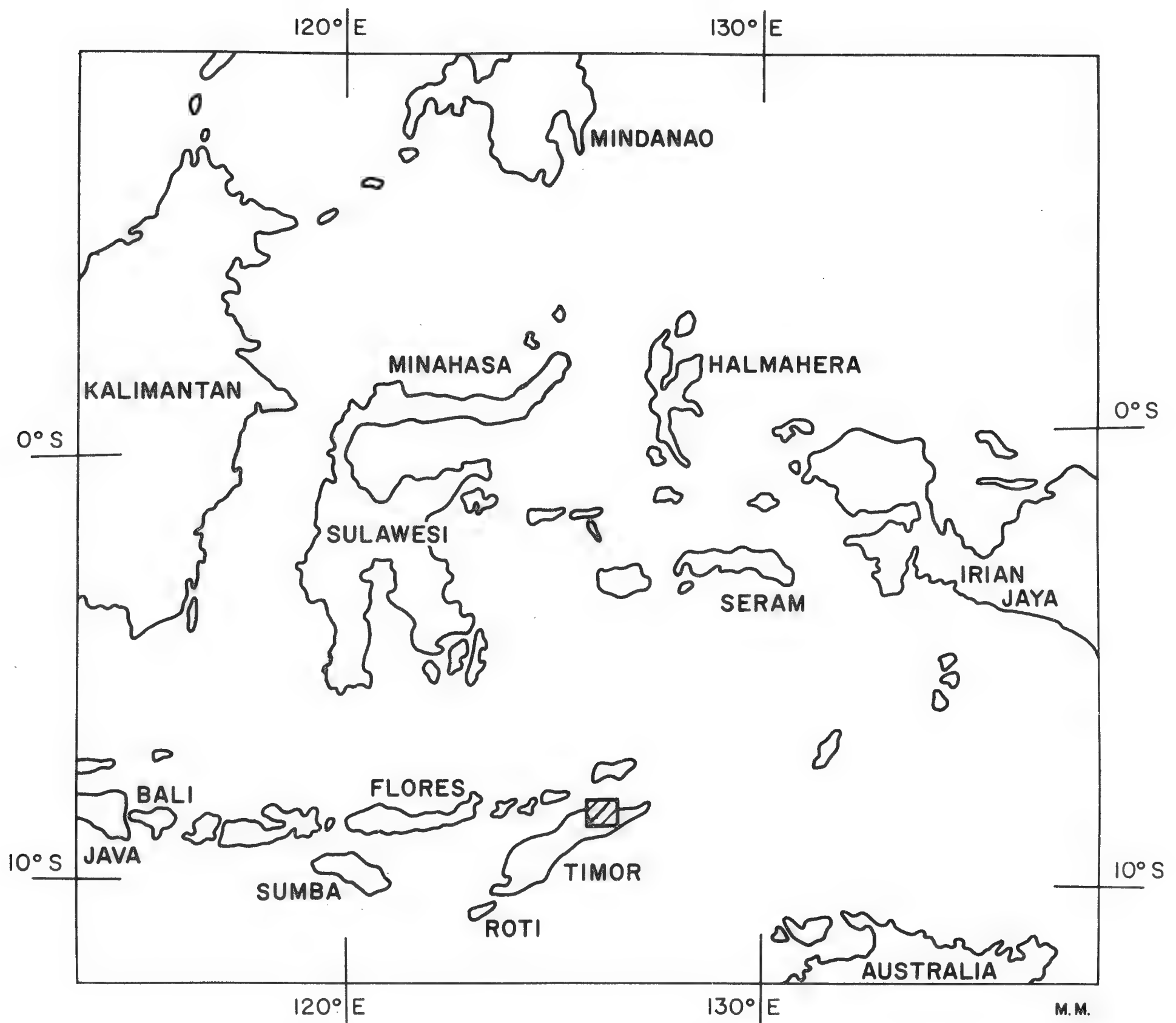


Fig. 1. South-east Asia and East Timor. Inset shows the location of the sites.

#### THE ARCHAEOLOGY OF MOLLUSC UTILIZATION IN INDONESIA

Molluscs have been recorded from many coastal archaeological sites in Indonesia. Extensive mounds of estuarine molluscs have been discovered along the west coast of Sumatra (van Heekeren 1972, pp. 85–92) which have been dated to at least 6th millennium BC (Bronson & Glover 1984, p. 43). In Java, Sulawesi and Irian Jaya some investigation has also been made of the economic value of molluscs to ancient man (Willems 1939, Glover 1981, van Bentham Jutting 1940, Heffernan 1980).

In a region so dominated by the sea, molluscs were always an important part of coastal economies, providing food and raw material for artefacts, although archaeologically it is not always easy to distinguish their particular function. In prehistoric sites in Timor *Nautilus*, *Oliva*, and *Trochus* were used for the manufacture of beads and *Tridacna* were polished to form small adzes (Glover 1972, p. 191) but probably most of the molluscs in the Timor sites, as elsewhere in Indonesia, were carried in as food, particularly *Haliotis*, *Nerita*, *Strombus* and *Turbo* species. Given the distance of the rock shelters from the reef it is unlikely that no more than an occasional individual mollusc was introduced into the deposit by chance. Molluscs did not contribute large amounts of protein to the diet of ancient communities but, as in many coastal economies, they provided a regularly available, and



# GLOVER: PREHISTORIC UTILIZATION OF MOLLUSCS

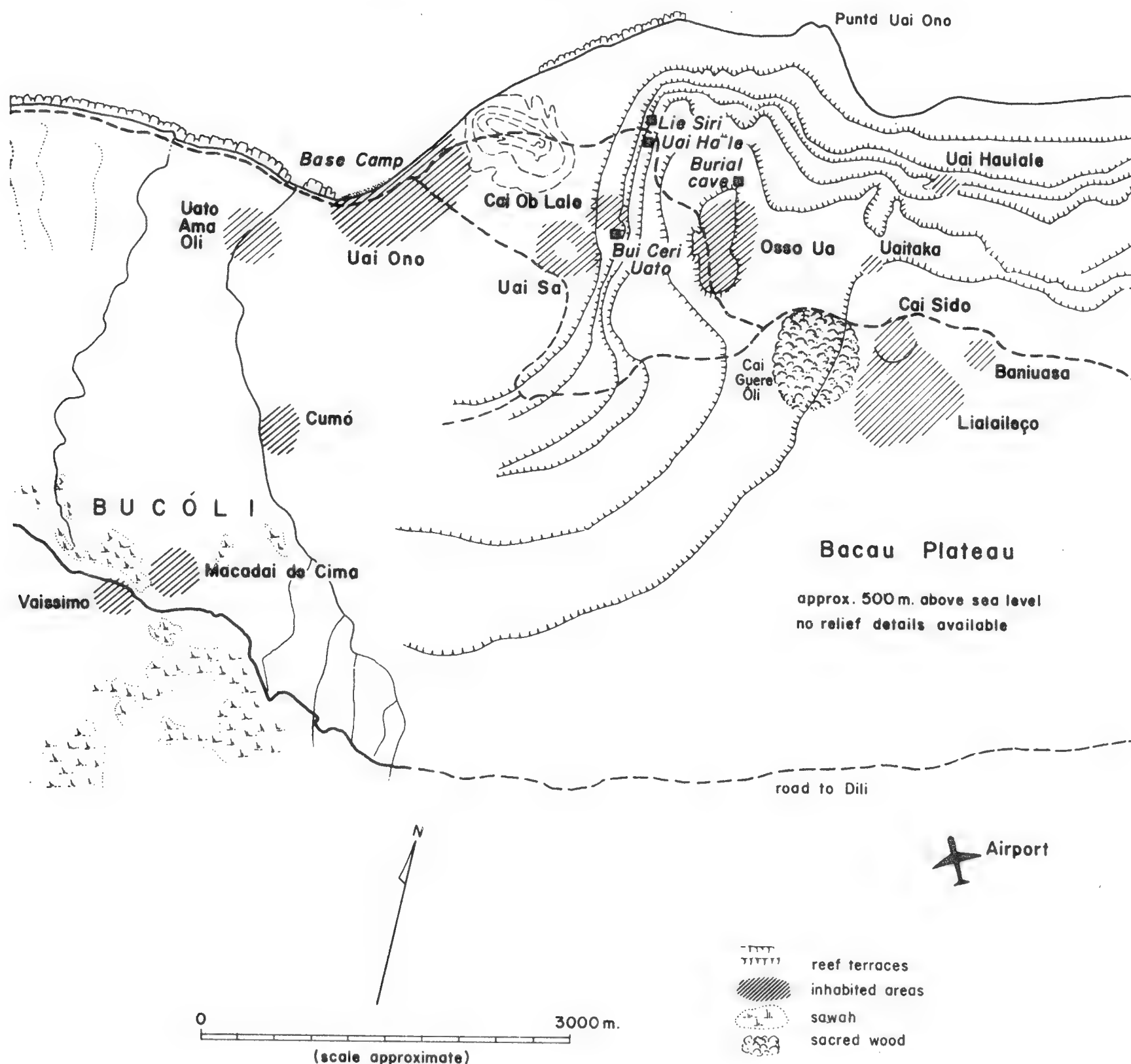


Fig. 2. Location of the archaeological sites, Lie Siri and Bui Ceri Uato on the raised reef terraces of the Baucau Plateau, East Timor.

generally reliable and palatable resource, which could be certainly collected when hunting and crops had failed, and as tasty and nutritious additions to a basically carbohydrate diet (Meehan 1982, p. 159). Molluscs are still regularly collected from the fringing reef in Timor, near the sites described in this report and these reefs have suffered human exploitation for nearly 8000 years. Evidence from Pleistocene terrace deposits elsewhere on the island indicates that man has been present as an active predator for very much longer than this; perhaps as long as 100,000 years (Glover 1973).

The molluscs described here were recovered from two excavations in small limestone rock shelters on the north coast of East Timor, Indonesia (Figs 1, 2). The sites are situated on raised Pleistocene reef terraces and are approximately 0.5 km from and between 100 m and 250 m above the existing fringing reef. The reef supports a typical Indo-West Pacific shallow water reef fauna, characteristic of exposed to moderately exposed shores. The reef platform is narrow with a maximum width of about 100 m and it is discontinuous along this part of the coast, with deep water occurring close to the reef edge. There is also a narrow rocky shore formed from partially raised ancient coral reef terraces, which supports an upper intertidal fauna. There has been no work on the coastal ecosystems of East Timor and unfortunately we have no site specific data with which to compare the results from the archaeological sites; however general comparison can be made with other better documented Indo-West Pacific intertidal communities.

A summary of the cultural and chronological sequence at the two coastal sites known as Lie Siri (code TL) and Bui Ceri Uato (code TB) is given in Fig. 3 and further information can be found in Glover 1972. Radiocarbon dating has established that the sites were occupied from approximately 8000BP to 500BP and although we cannot be certain of this, there is no archaeological evidence for long periods of abandonment; rather a steady low frequency of site occupation is envisaged.

In the lowest levels of the site were stone tools and bones of birds, native rodents, bats, fish, reptiles as well as mollusc shells and these remains clearly indicate a hunting and gathering community. Gradually, with the exception of molluscs, most of these animals were replaced by an introduced fauna accompanied by pottery from about 4500 years ago. Although direct evidence for plant cultivation is not available until more recent times, this change in the sequence of food remains and artefacts may be the result of the arrival of techniques of cultivation and animal husbandry. The present mammalian fauna includes Rusa deer, civet cat, macaque, and cuscus as well as domesticated goats, sheep, pigs, cattle, buffaloes, horses and dog. There is strong archaeological evidence that after their arrival the native fauna suffered a progressive depletion in variety and at least four genera of giant native rats appear to have become extinct (Glover 1972).

Molluscs were present from the earliest to latest levels of the site and there is some evidence that molluscs were more abundantly collected and that there was a greater range

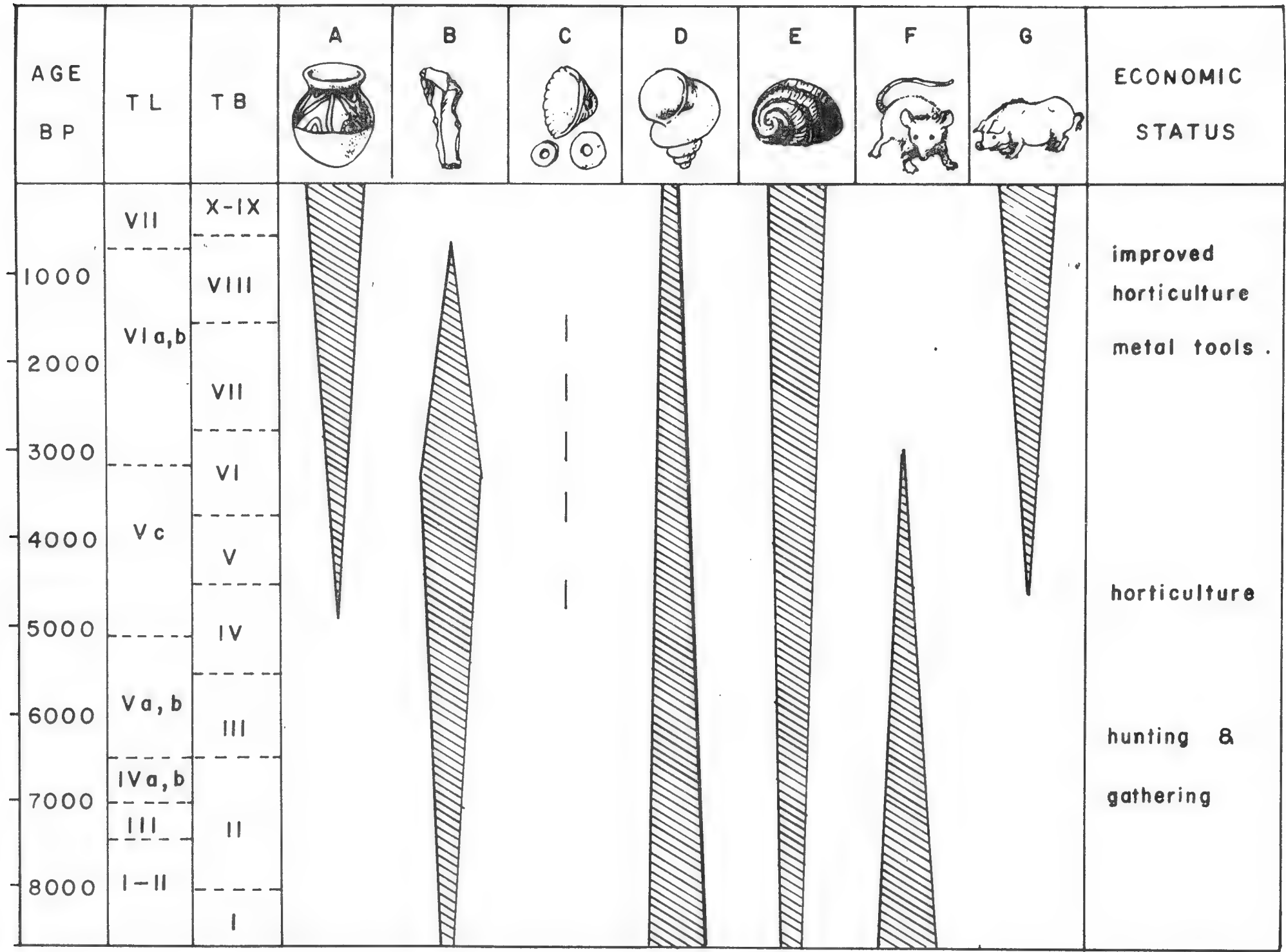


Fig. 3. Cultural and chronological correlations of the sites Lie Siri (TL) and Bui Ceri Uato (TB). A = pottery, B = stone artefacts, C = shell artefacts, D = terrestrial molluscs, E = marine molluscs, F = endemic fauna, particularly native rodents, G = introduced fauna, including domesticated animals. Time scale is based on C-14 dates.

GLOVER: PREHISTORIC UTILIZATION OF MOLLUSCS

TABLE 1

Distribution of molluscs at Lie Siri, horizons Ia–VII. The table lists the percentage of individuals of each species by horizon.

Species	Horizons												m.n.i.
	VII	VIb	VIa	Vc	Vb	Va	IVb	IVa	III	II	Ib	Ia	
MARINE													
Gastropoda													
HALIOTIDAE													
Haliotis varia L.	13	9	21	32	33	13	23	30	23	17	13	15	859
PATELLIDAE													
Cellana?radiata													
Born	2	1	1	1	2	6	2	1	3	2	*	4	56
Cellana sp.	—	—	—	—	—	—	—	—	—	—	—	*	1
Acmaea sp.	*	1	*	*	*	5	—	—	—	—	—	—	18
fam. Patellidae	1	*	*	—	*	—	—	—	—	—	*	—	10
TROCHIDAE													
Trochus maculatus L.	3	3	1	2	1	3	1	2	1	1	1	4	67
Trochus niloticus L.	—	—	—	*	—	—	—	—	—	—	—	—	1
Trochus ?squarrosus													
Lamarck	—	—	—	*	—	—	*	—	—	—	—	*	3
Trochus sp.	—	*	—	—	*	—	—	—	—	—	*	—	4
Tectus ?pyramis													
Born	—	*	—	—	—	—	*	—	—	—	—	—	4
Monodonta sp.	—	—	*	—	—	—	—	—	—	—	—	—	1
TURBINIDAE													
Turbo marmoratus L.	—	—	—	—	—	2	*	—	—	—	—	—	4
Turbo setosus													
Gmelin	5	2	1	2	2	1	1	—	3	5	5	1	98
Turbo chrysostomus L.	3	2	2	2	—	1	*	—	1	—	*	—	48
NERITIDAE													
Nerita albicilla L.	—	—	*	—	—	—	—	—	—	—	—	—	2
Nerita costata													
Gmelin	9	10	8	6	3	1	2	1	1	3	2	—	196
Nerita exuvia L.	*	*	—	—	—	—	*	—	—	—	—	—	3
Nerita ?chameleon L.	—	—	*	—	—	—	—	—	—	—	—	—	1
Nerita grossa L.	1	—	*	—	—	—	1	—	—	1	—	—	7
Nerita plicata L.	24	34	30	23	6	7	10	25	15	8	9	4	748
Nerita polita L.	*	1	1	1	1	2	1	1	—	2	1	2	36
Nerita ?polita L.	—	1	—	*	—	—	—	2	1	—	—	—	11
Nerita textilis													
Gmelin	—	—	—	—	—	1	1	5	3	5	12	13	97
Nerita undata L.	1	—	1	1	2	2	3	2	4	6	3	4	72
Nerita ?undata L.	*	*	—	—	*	—	—	—	—	—	—	—	5
Neritopsis radula (L.)	—	—	*	*	—	—	—	—	—	—	—	—	2
LITTORINIDAE													
Littorina undulata													
Gray	—	*	—	—	—	—	—	—	—	—	—	—	1
Tectarius grandinatus													
(Gmelin)	—	1	*	*	1	—	*	—	—	6	1	—	25
Tectarius tectumpersicum													
(L).	—	—	*	—	—	—	—	—	—	—	—	—	1
Tectarius pagodus (L.)	1	6	3	4	1	1	3	4	3	3	2	4	120
Echininus cumingii													
(Philippi)	*	—	—	—	—	—	—	—	—	—	—	—	1

\* =<0.5%

Species	Horizons												
MARINE	VII	VIb	VIa	Vc	Vb	Va	IVb	IVa	III	II	Ib	Ia	m.n.i.
THIARIDAE													
<i>Melanoides tuberculata</i> (Müller)	—	—	*	—	—	—	—	—	—	*	—	—	2
<i>Melanoides</i> sp.	—	—	—	*	—	2	*	—	—	1	—	—	8
POTAMIDIDAE													
<i>Terebralia palustris</i> (L.)	—	—	*	*	1	8	1	—	1	—	—	—	28
<i>Terebralia sulcata</i> Born	—	*	*	*	1	3	1	—	—	—	—	—	17
<i>Terebralia</i> sp.	—	—	—	—	*	3	*	—	—	—	—	—	8
CERITHIIDAE													
<i>Clypeomorus</i> sp.	—	—	—	—	—	—	—	—	—	—	*	—	1
fam. Cerithiidae	—	—	*	—	—	—	—	—	—	—	—	—	2
STROMBIDAE													
<i>Strombus aurisdianae</i> L.	*	—	*	—	—	—	—	—	—	—	—	—	4
<i>Strombus decorus</i> Roeding	3	1	1	*	—	—	—	*	—	—	—	—	20
<i>Strombus lentiginosus</i> L.	*	—	—	—	—	—	—	—	—	—	—	—	1
<i>Strombus luhuanus</i> L.	3	2	1	1	—	—	—	*	—	—	—	—	31
<i>Strombus maculatus</i> Sowerby	—	—	—	*	—	—	—	—	—	—	—	—	1
<i>Lambis crocata</i> Link	—	—	—	—	—	—	*	—	—	—	—	—	1
<i>Lambis</i> sp.	—	—	*	—	—	—	—	—	—	*	—	—	3
CYPRAEIDAE													
<i>Cypraea arabica</i> L.	*	*	—	—	—	—	—	—	—	—	—	—	4
<i>Cypraea caputserpentis</i> L.	2	2	1	2	1	—	3	—	1	—	—	—	58
<i>Cypraea depressa</i> Gray	*	*	*	—	—	—	—	—	—	—	—	—	3
<i>Cypraea helvola</i> L.	*	—	—	—	—	—	—	—	—	—	—	—	1
<i>Cypraea moneta</i> L.	*	—	—	—	—	—	—	—	—	—	—	—	1
<i>Cypraea tigris</i> L.	*	—	—	—	—	—	—	—	—	—	—	—	1
fam. Cypraeidae	*	1	*	*	1	—	—	—	—	—	—	—	11
BURSIDAE													
<i>Bursa</i> sp.	—	—	*	*	—	—	—	—	—	—	—	—	2
CYMATIIDAE													
fam. Cymatiidae	—	—	—	—	—	—	—	—	—	—	*	—	1
MURICIDAE													
<i>Thais armigera</i> Link	—	*	1	1	1	1	*	—	—	—	*	—	17
<i>Thais savignyi</i> (Deshayes)	1	2	1	1	1	1	1	2	1	1	2	1	51
<i>Thais</i> sp.	*	—	*	*	*	—	1	—	1	—	*	—	12
<i>Mancinella mancinella</i> (L.)	*	1	*	*	1	1	1	—	—	—	—	—	18
<i>Purpura panama</i> (Roeding)	—	—	*	—	—	—	—	—	—	—	—	—	1
<i>Drupa morum</i> (Roeding)	*	*	—	—	—	—	*	—	—	—	—	—	3
<i>Drupa ricinus</i> (L.)	—	1	—	*	*	—	*	—	—	—	—	—	9
<i>Chicoreus brunneus</i> (Link)	—	—	—	*	—	—	—	—	—	—	—	—	1
fam. Muricidae	—	—	—	*	—	—	—	—	—	—	—	—	4
NASSARIIDAE													
<i>Nassarius ?fida</i> (Reeve)	—	—	—	—	—	—	*	—	—	—	—	—	1
<i>Nassarius</i> sp.	—	—	—	—	*	—	—	—	—	—	—	—	1



GLOVER: PREHISTORIC UTILIZATION OF MOLLUSCS

Species	Horizons												
	VII	VIb	VIa	Vc	Vb	Va	IVb	IVa	III	II	Ib	Ia	m.n.i.
MARINE													
BUCCINIDAE													
Cantharus undosus L.	—	—	—	—	*	—	—	—	—	—	—	—	1
FASCIOLARIIDAE													
Leucozonia smaragdula L.	—	*	—	—	—	—	—	—	—	—	—	—	1
Leucozonia sp.	—	*	—	—	—	—	—	—	—	—	—	—	1
Pleuroploca filamentosa (Roeding)	*	—	—	—	—	—	—	—	—	—	—	—	1
VASIDAE													
Vasum turbinellus (L.)	—	—	—	—	*	—	—	—	—	—	—	—	1
OLIVIDAE													
Oliva ?oliva L.	—	—	—	*	*	—	*	—	—	—	—	—	5
Oliva ?carneola Gmelin	—	—	*	*	—	—	—	—	—	—	—	—	2
VOLUTIDAE													
Melo sp.	—	—	—	—	*	—	—	—	—	—	—	—	1
CONIDAE													
Conus ebraeus L.	*	—	—	—	—	—	—	—	—	—	—	—	3
Conus ?imperialis L.	—	*	—	—	—	—	—	—	—	—	—	—	1
Conus marmoreus L.	1	1	1	1	—	—	*	—	—	—	—	—	16
Conus miles L.	—	—	*	—	—	—	—	—	—	—	—	—	1
Conus spectrum L.	—	*	—	—	—	—	—	—	—	—	—	—	1
Conus virgo L.	*	—	—	—	—	—	—	—	—	—	—	—	1
Conus sp.	*	—	*	1	—	—	—	—	—	—	*	—	8
PYRAMIDELLIDAE													
fam. Pyramidellidae	*	—	—	—	—	—	*	—	—	—	—	—	3
Bivalvia													
ARCIIDAE													
Andara sp.	*	—	—	—	—	—	—	—	—	—	—	—	1
Barbatia ?fusca Bruguère	*	—	—	—	—	—	—	—	—	—	—	—	2
OSTREIDAE													
Ostrea sp.	—	*	*	*	1	—	*	—	1	1	*	—	13
CARDIIDAE													
Trachycardium alternatum Sowerby	—	—	*	—	—	—	—	—	—	—	—	—	1
TRIDACNIDAE													
Tridacna maxima (Roeding)	1	2	*	*	—	1	—	—	—	—	—	—	13
Tridacna sp.	*	*	—	—	—	—	—	—	—	—	—	—	4
Hippopus hippopus L.	1	*	*	*	—	—	—	—	—	—	—	—	7
CORBICULIDAE													
Geloina sp.	3	1	1	2	3	1	2	—	1	1	—	—	53
VENERIDAE													
Meretrix sp.	—	—	—	—	—	—	*	—	—	—	—	—	1
Periglypta sp.	*	—	*	—	—	—	—	—	—	—	—	—	2
GARIIDAE													
Asaphis deflorata (L.)	—	—	—	—	—	—	*	—	—	—	—	—	1
CEPHALOPODA													
Nautilus pampilius L.	2	1	1	*	1	—	1	1	—	1	—	—	27
POLYPLACOPHORA													
<sup>1</sup> Chiton	5	5	8	8	15	28	17	20	28	15	35	40	631

<sup>1</sup> Chiton only survive in the cave deposit as individual plates. Percentage frequency of individuals in the table is indicated by the number of end plates divided by two and expressed as a percentage of molluscs in each horizon.

Species	Horizons												
	VII	VIb	VIa	Vc	Vb	Va	IVb	IVa	III	II	Ib	Ia	m.n.i.
<i>TERRESTRIAL</i>													
<i>Gastropoda</i>													
CAMAENIDAE													
<i>Amphidromus contrarius</i> (Mueller)	1	1	1	1	1	—	1	2	—	4	3	1	49
<i>Chloritis</i> sp.	7	4	4	5	10	4	12	—	3	8	4	4	247
ARIOPHANTIDAE													
	*	1	*	*	*	2	2	2	3	—	3	—	56
HELICINIDAE													
<i>Geophorus oxytropus</i> (Sowerby)	*	*	1	*	1	—	1	—	1	—	—	—	21
CYCLOPHORIDAE													
<i>Cyclotus succinctus</i> v. Martens	—	—	*	*	*	—	2	—	—	1	—	—	15
other land snails	1	*	*	*	4	2	—	—	—	1	1	—	32
total individuals	312	399	611	655	417	157	507	127	144	139	470	114	4052
species richness	51	46	56	47	39	27	45	15	22	25	26	16	

of species in the middle and later levels. There is supporting evidence from the analysis of pottery and stone artefacts that there was increased use of the site after 4500 years ago and it is suggested that population increased after the establishment of horticulture.

Very few fish bones were found at either site, despite the proximity of the sea. Coastal foraging was confined almost entirely to molluscs and crustacea from the littoral. Modern Timorese are as reluctant to go to sea as it seems their ancestors were, and fish are caught only occasionally. This particular dependence on the littoral is relevant to the intensification of use of intertidal molluscs in the later levels of the site.

#### METHODS

The molluscs were sampled during the excavation from all levels of the two sites and these units were later combined in a series of archaeological horizons numbered I from the base. These horizons were grouped on the basis of chronology, cultural content and stratigraphy. Mollusc shells from the horizons were sorted into species where this was possible and the number of individuals counted. Most of the shells were quite fragmentary. Gastropod apertures tended to survive intact and these were counted to give a minimum number of individuals. Bivalves were uncommon in both sites and a subjective estimate of individual numbers was made by counting surviving valves. Both sites had a similar suite of species and for reasons of space, only the data from Lie Siri is shown in Table 1.

Unbroken *Haliotis varia* were common throughout both sites and it was possible to measure maximum length. Otherwise, there were few gastropods complete enough to measure the entire shell and the maximum aperture height was used to provide a rough size index. To confirm that aperture height was indeed a reasonable measure of overall size, measurements were made of a sample of live collected *Nerita textilis* from Salalah, Oman. A correlation coefficient of 0.93 was obtained which implies that aperture height is a fair index of total size, at least for this species and possibly for most gastropods.

Aperture size measurements were made of some of the more common gastropods, namely, *Nerita plicata*, *Nerita textilis*, *Turbo setosus* and *Turbo chrysostomus* but these data are rather incomplete because of the low numbers of measureable individuals.

The numbers of individuals of each species for each horizon were recorded on a data matrix adapted from the Cornell Ecology Programme series. The data was run on Twinspan, a cluster analysis programme which placed the horizons in positively correlated groups (Gauch 1982, Hill 1979).

## RESULTS

The results of the analysis of mollusc samples are remarkably consistent for both sites that were studied, although the number of samples at Bui Ceri Uato is rather small. However, the close correlation of the sites helps to support the interpretations that have been suggested. A great diversity of molluscs was found, in all, over one hundred species, which are listed in Table 1. The most abundant groups were intertidal reef gastropods of the families Haliotidae, Neritidae, Conidae, Muricidae, Turbinidae, and Trochidae, and members of these families were found throughout the archaeological sequence. The reef-derived molluscs divide into two main categories, those which inhabit intertidal rocky cliffs and those from the reef flats which are exposed only at spring tide periods. There was also a great diversity of less abundant reef species as well as numbers of potamid gastropods and corbiculid bivalves from mangrove mud flats. There were also numbers of terrestrial molluscs, listed in Table 1.

A cluster analysis shown in the dendrogram plot (Fig. 4) distributes the mollusc data into two main groups, that is horizons VII – IVb and IVa–Ia. The erratic position of horizon Va is probably related to the small sample size from that horizon and otherwise all the horizons are more or less in stratigraphic order. At both sites there were some changes in species composition after 6000 years ago, although this change is less clear at Bui Ceri Uato. At Lie Siri the obvious differences were the increased variety of reef flat species, especially Conidae and Cypraeidae. Shell artefacts appear in the upper horizons and it may be that new species were brought to the sites for the first time for the manufacture of beads. The upper horizons had a greater density by volume of shells than the lower horizons and it appears that the site was more intensively used in that period which might also account for the greater range of species from the reef. There was a small proportional decrease in numbers of individuals of reef flat species in the upper horizons in contrast to Neritidae from the rocky shore, which showed a proportional increase in numbers of individuals in the upper horizons.

Neritidae were examined in greater detail because they were reasonably abundant throughout the sequence at both sites. Species distribution and abundance over time is shown in Figs. 5 and 6, and it is obvious that a similar pattern of distribution exists for both sites. Thus it is not unreasonable to assume that the particular abundance of species in the samples does reflect changes in local populations at various times. All the Neritidae species found in the site are common Indo-West Pacific species on rocky shores. *Nerita plicata* and *N. costata* are usually quite abundant but are smaller than the other species and less rewarding food species. However, towards the end of the archaeological sequence these two species are the most common while the larger *Nerita polita* and *N. undata* have decreased in numbers. The largest species, *Nerita textilis*, occurs abundantly in the earliest levels but not thereafter.

Throughout the Indo-West Pacific *Nerita textilis* is a common species inhabiting exposed rocky shores, where in the absence of human predation they can occur in densities of up to 12–13 individuals per square metre (Hughes 1971). It is one of the largest species of *Nerita* and unlike some of the smaller species does not usually seek the shelter of rock crevices at low tide. These two factors combine to make it an obvious and easily collected animal although there is no other record of its use as food in Indonesia either archaeologically or

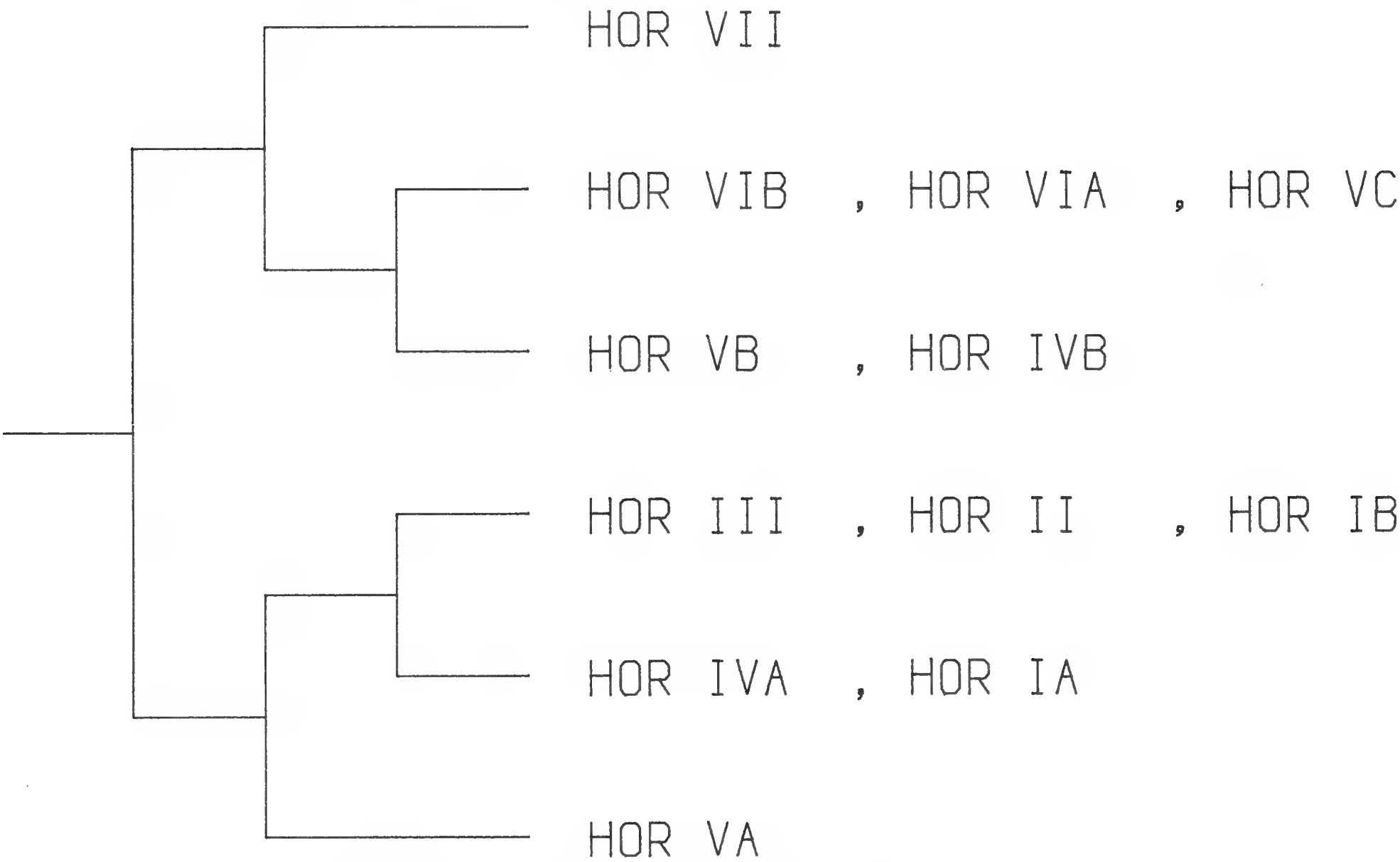


Fig. 4. Dendrogram of mollusc distribution in horizons I-VII at Lie Siri.

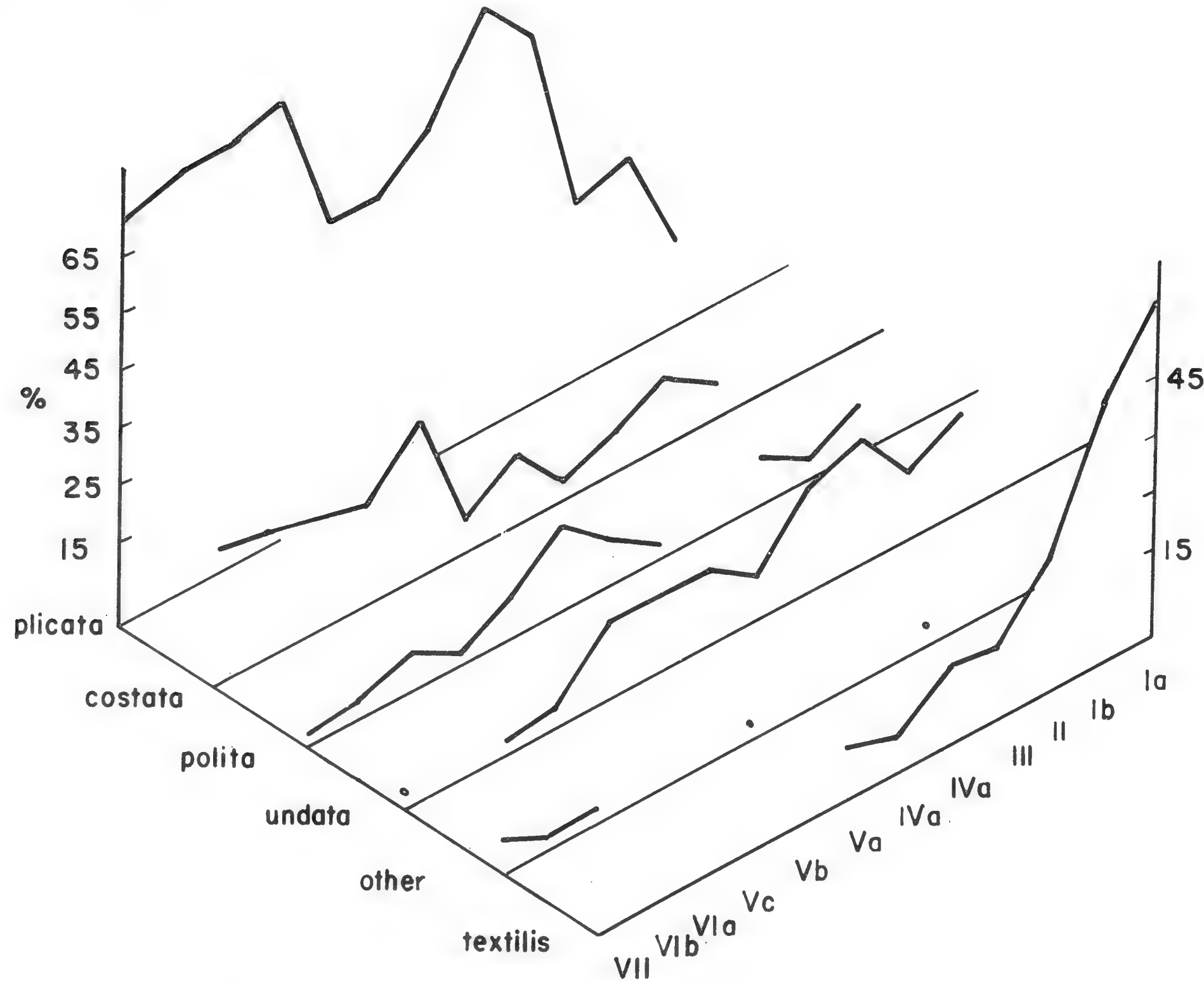


Fig. 5. Percentage of *Nerita* species at Lie Siri in horizons I-VII.



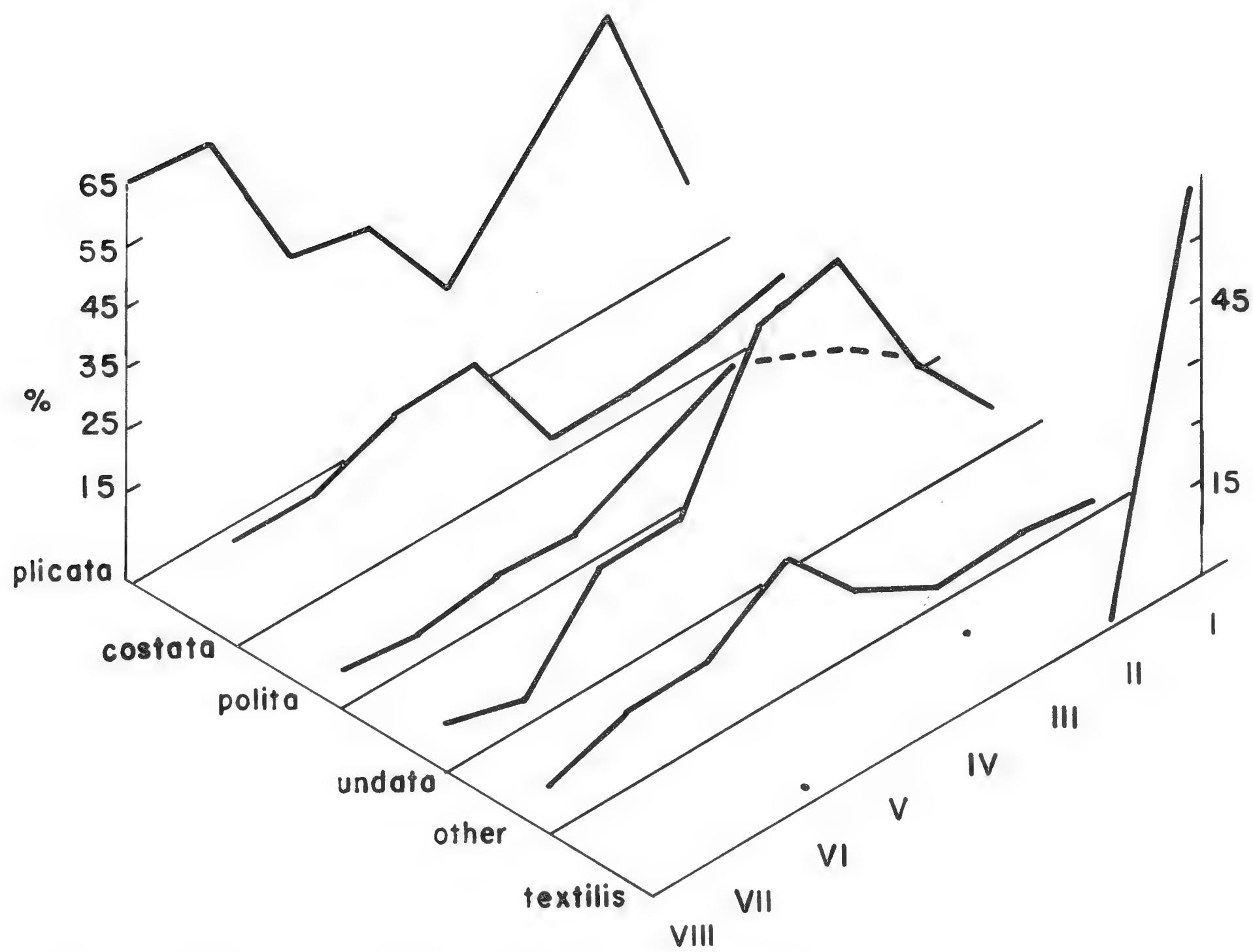


Fig. 6. Percentage of *Nerita* species at Bui Ceri Uato in horizons I–VIII.

TABLE 2

Measurement of mean aperture size of *Nerita* species from four Indo-Pacific localities.

<i>Nerita textilis</i>		$\bar{x}$ mean aperture height in mm.									
TB		TL		Mombasa*		Salalah*		Aldabra*		Adlabra*	
<i>n</i>		<i>n</i>		<i>n</i>		<i>n</i>		<i>n</i>		<i>n</i>	
$\bar{x}$		$\bar{x}$		$\bar{x}$		$\bar{x}$		$\bar{x}$		$\bar{x}$	
34		7		27		24		10		18	
11.7		12.3		10.1		12.7		21.7		15.3	

\*specimens held in B.M. (NH), London  
Aldabra a = Dune d'Messe  
Aldabra b = Dune Jean Louis

ethnographically. However in the Seychelles it is far less preferred as a food species than *Nerita polita* (Taylor pers comm).

Aperture size measurements of some widely distributed populations of *Nerita textilis* are given in Table 2. The sizes of *N. textilis* from the archaeological sites are comparable with some present day populations from near human habitation in Oman and India. Species of *Nerita* from Aldabra, which are not exploited, are considerably larger.

Measurements of *Haliotis varia* are given in Fig. 7. At both sites there was a decline in mean size after the first two horizons with the lowest mean size in the upper horizons.

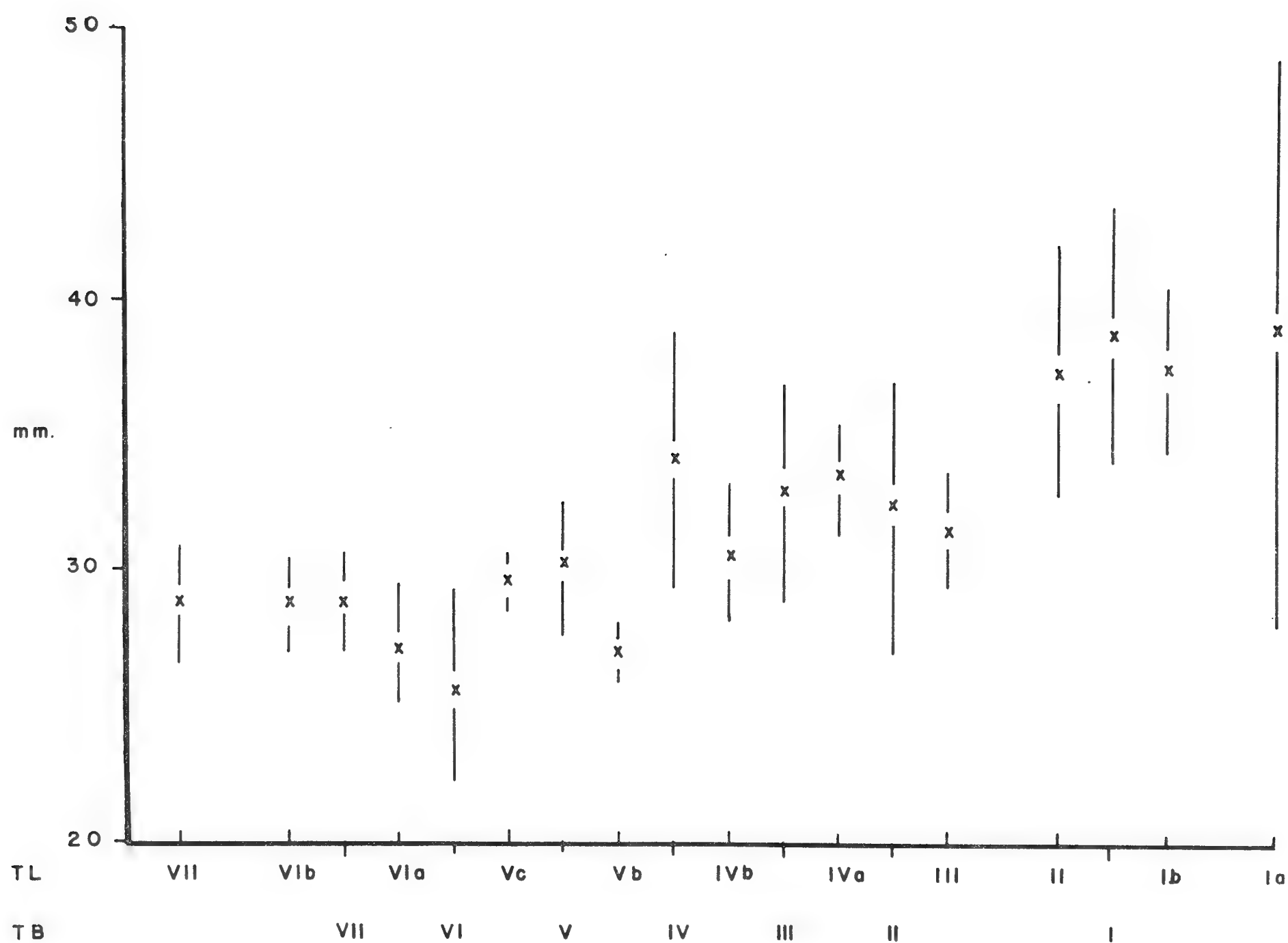


Fig. 7. Mean length (mm) and 95% confidence limits of mean of *Haliotis varia* from two sites, Lie Siri (TL) and Bui Ceri Uato (TB).

TABLE 3

Measurement of mean aperture size of *Nerita* species from Bui Ceri Uato.

TB *Nerita* spp.  $\bar{x}$  aperture size in mm., m.n.i.

Horizon	<i>textilis</i>		<i>plicata</i>		<i>costata</i>		<i>undata</i>		<i>polita</i>	
	m.n.i.	$\bar{x}$	m.n.i.	$\bar{x}$	m.n.i.	$\bar{x}$	m.n.i.	$\bar{x}$	m.n.i.	$\bar{x}$
VIII	1	—	11	10.1	3	—	1	—	1	—
VII	—	—	16	8.7	4	—	1	—	1	—
VI	1	—	12	9.0	7	—	6	10.0	2	—
V	—	—	6	—	4	—	3	—	1	—
IV	3	—	4	8.1	1	—	10	10.9	3	—
III	—	—	24	8.0	2	—	33	10.4	13	11.3
II	8	—	40	7.6	4	—	18	10.1	10	13.3
I	34	11.7	7	8.7	5	—	3	—	3	—

Similarly for *Turbo setosus* (Fig. 8) there is a reduced mean size after the first horizons. Additionally, qualitative observations of *Strombus* species also suggested a similar size reduction in the upper horizons. In the case of the smaller *Nerita* species, *N. plicata*, *N. costata*, *N. undata*, and *N. polita* these have similar mean aperture heights throughout the sequence at both sites, although *N. undata* and *N. polita* were far less abundant in the upper horizons (Table 3).

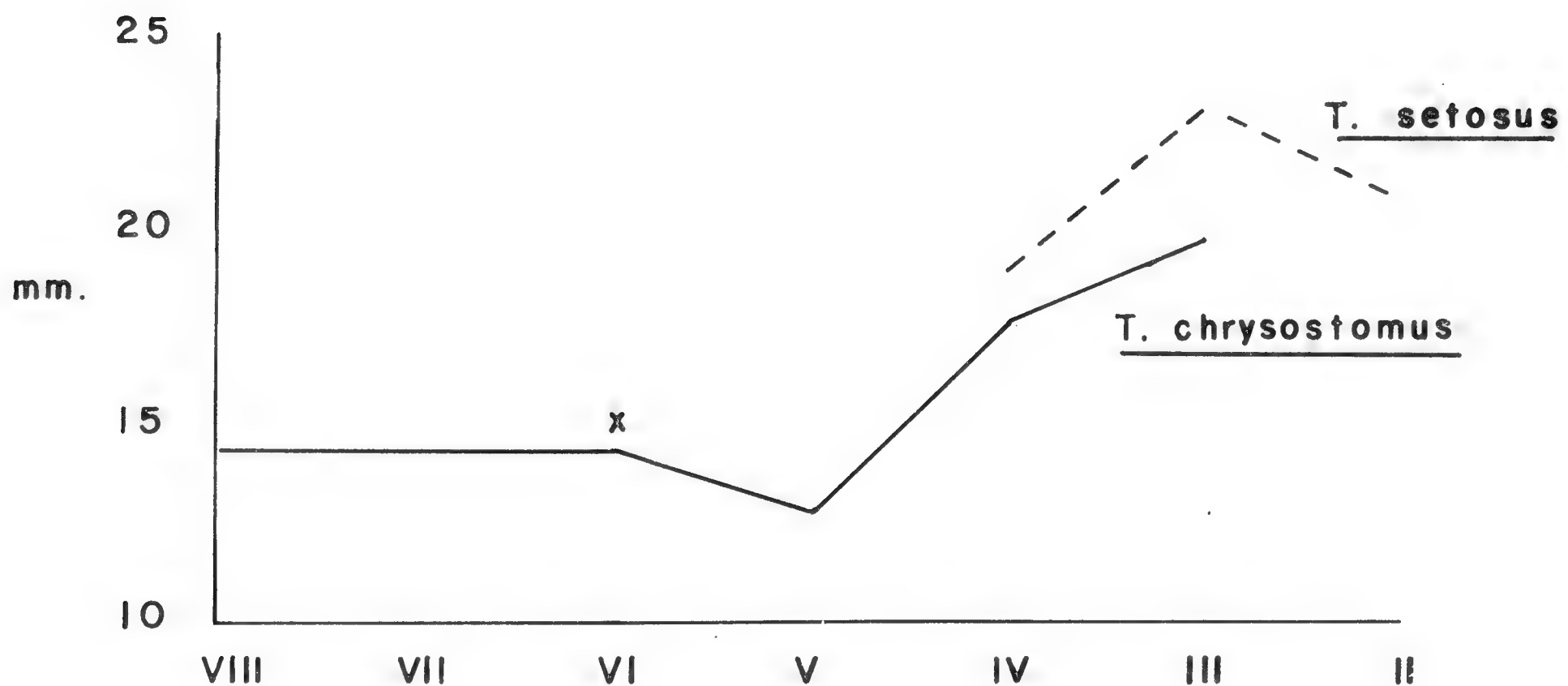


Fig. 8. Mean aperture height (mm) of *Turbo setosus* and *Turbo chrysostomus* from Bui Ceri Uato. x = mean aperture height of *Turbo chrysostomus* from Horizon Vc at Lie Siri.

### DISCUSSION

There are three general conclusions that could be drawn from the evidence of the mollusc samples in these two Timorese sites. Firstly, the sites contain an exceptional diversity of species, that could perhaps be found adjacent only to a tropical coral reef. However, most of the species are not especially abundant in the site. Secondly, the sites cover a period of approximately 8000 years during which time there were no major changes in the long term pattern of mollusc collection. Molluscs from the reef and the intertidal rocky shore were always present in the site. Finally, there were some small changes in species abundance and distribution. The upper horizons at both sites do contain a much greater diversity of species from the reef. There is a dramatic decline in the frequencies of *Nerita textilis* at both sites. It is the only species that is common in the lower horizons but uncommon or absent from the upper. *Nerita plicata* and *N. costata* become much more common compared to other *Nerita* species in the upper horizons. There is also some evidence that the size range of a few of the more abundant molluscs is reduced in the upper horizons.

These changes in the pattern of mollusc utilization could be caused by a number of factors which include; natural fluctuations in the abundance of species controlled by extrinsic environmental forces; human exploitation causing species depletion; and cultural changes. The stability of most of the molluscs species throughout the sequence implies that there was no large scale change in the local coastal environment. In contrast, the evidence from the artefacts and animal bones show that major cultural changes did take place (Fig. 3), which may have meant intensification of use of all local resources.

For the occupiers of these Timorese caves the only important marine resources were from the narrow rocky shore and the reef flat. In contrast to other habitats, such as estuaries, tropical reefs are remarkably diverse, but individual populations are not abundant. The evidence from the sites is that a great diversity of species were brought to the caves, but only a few species were especially frequent. In other words, man seems to have adopted the 'best' strategy in exploiting the reef, that is to generalise, rather than specialise on a few target species (Hughes 1980). Clearly, predator specialisation on one or two species on a tropical coral reef could lead to depletion of the preferred prey. In particular, the disappearance of *Nerita textilis* may be the result of over-exploitation during the early occupation of the sites.

Some recent studies have examined the effects of intensive human predation on molluscs. A study in Chile looked at the delicate balance between the abundance of macro-algae, the density of the herbivorous gastropod, *Fissurella picta*, and predation by man (Moreno *et al.* 1984). This paper highlights two of the effects that exploitation by man may have. These are depletion of the preferred species and a reduction of size range of the population. Under conditions of heavy human predation the population of *Fissurella picta* was depleted and macro-algae became abundant, while the reverse occurred in conditions of low human predation. Data on size showed that most individuals of the species which survived moderate to heavy predation were less than 4 cm in length. In a test situation where man was excluded from a nature reserve from 1978, more than half the individuals had reached more than 4 cm in length by 1981. Size reduction and depletion related to human predation have also been recorded for two limpet species, *Patella concolor* and *Cellana capensis* in South Africa (Branch 1975). *Strombus luhuanus* populations have been studied along the New Guinea coast near Port Moresby to assess the effect of human exploitation. Heavily fished populations show a marked reduction in age range and overall size with a dominance of younger age classes, and specimens from coastal middens showed many of the features of an exploited population (Swadling 1977). Similar reduction in size range has been reported for the mussel *Perna perna* from coastal sites in South Africa (Hall 1980).

In the absence of comparative site-specific archaeological and ecological data, it is unsatisfactory to attempt precise conclusions for the evidence from the Timorese sites. Future archaeological work on coastal sites in Indonesia will certainly provide evidence for the ancient use of molluscs. We may also expect to find that human predation in other locations has, to some extent, altered the structure of the populations of the preferred species and indirectly affected other organisms in the habitat. This a dimension which ecological studies of modern populations must take into account.

#### ACKNOWLEDGEMENTS

Dr. I. C. Glover, Institute of Archaeology, London and Dr. J. D. Taylor, British Museum (Natural History), gave much help and encouragement during the preparation of this paper. Mr. F. Naggs, British Museum (Natural History) identified the terrestrial molluscs and Mrs. A. Lehar-Graham provided the illustrations for Fig. 3.

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# TWO SMALL SPECIES OF THE GENUS *RETINELLA* FROM THE WESTERN ALPS (MOLLUSCA: PULMONATA: ZONITIDAE)<sup>1</sup>

FOLCO GIUSTI<sup>2</sup>, ALBERTA BOATO<sup>3</sup> AND MARCO BODON<sup>4</sup>

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**Abstract:** A few taxa of the Zonitidae from N-W Italy may be presently confused, because of the shell characters, with *Aegopinella pura* (Alder). However, they are clearly distinguished from the latter by anatomical features. These features suggest their being placed in the genus *Retinella* Fisher. Thus *Retinella pseudoaegopinella* is described as a new species, and *Hyalinia stabilei* Pollonera is confirmed as a good *Retinella* species. These two *Retinella* show anatomical and shell characters which do not fit in with those of the subgeneric taxa now in use. This constitutes an indication that the validity of subgenera should be reconsidered.

## INTRODUCTION

During a series of field trips (1977–1981) designed to collect informations for use in a revision of the land and freshwater malacofauna of the Ligurian Alps (Western Alps) (Giusti *et al.* 1985, Boato *et al.* 1985) we happened upon a small Zonitidae superficially very similar to *Aegopinella pura* (Alder). Nevertheless, as soon as its genital tract was studied, it was clear that it belonged to the genus *Retinella* Fisher, 1877. The shell of *A. pura* (Fig. 4D) is nearly indistinguishable from that of the two *Retinella* studied here (Fig. 5 A–B). With a thorough analysis it can be, at times, recognized by the smaller frontal outline, the paler horny-yellow colour, the more oval aperture and the deeper sutures. Shells that could be referred to the same species were collected in 13 different sites in the Ligurian Alps. Only in four of these sites, however, were we able to find living adult specimens allowing an anatomical study and therefore an irrefutable diagnosis. Contemporaneous field researches in the districts of M. Fenera (province of Vercelli, Northern Piedmont) and the Cottian Alps (Crissolo, province of Turin, Piedmont) brought our attention to other populations of the same species and so to suppose its distribution to be extended to the whole W-Alpine and W-pre-alpine district. In the same area *A. pura* does not seem to occur. This fact, besides reopening the problem of the actual distribution of *A. pura* in Italy, forced us to take into account some W-alpine taxa usually regarded as probable synonyms of *A. pura*. Two of these taxa were described using Italian material: *Hyalinia mixta* Westerlund, 1886 and *Hyalinia stabilei* Pollonera, 1886. In the literature *A. pura* is recorded in Italy, from the Alps to Gargano, and in Sardinia and Sicily (Alzona 1971, Riedel 1980). However, its presence is confirmed by anatomical evidence only for a few localities: Passo di Romezzano (North-Apennines, Parma, Emilia); M. Penna di Sumbra (Apuane Alps, Lucca, Tuscany) (Giusti & Mazzini 1970); Reatini Mountains (Central Apennines, Rieti, Latium) (Giusti 1971); Matese Mountains (Central Apennines, Campobasso, Molise); Foresta Umbra (Gargano, Foggia, Apulia); M. Pollino (Southern Apennines, Cosenza, Calabria); Bocognano (Corsica); M. Palai (Marghine Mountains, Bolotana, Sardinia).

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<sup>2</sup> Istituto di Zoologia, Università di Siena, Via Mattioli 4, I-53100 Siena, Italy; <sup>3</sup> Dipartimento di Biologia, Via Loredan 10, I-35100 Padova, Italy; <sup>4</sup> Via Niccolini 70, I-16166 Genova, Italy.

*H. mixta* has recently been regarded by Riedel (1983) as a junior synonym of *Nesovitrea hammonis* (Ström, 1765). The type specimen from M. Codeno (Esino, Como, Lombardy) preserved in the Museum of Natural History of Göteborg must undoubtedly be referred to the genus *Nesovitrea* because of the strong transverse striations on the shell surface. On the other hand, the type shell of *H. stabilei* Pollonera from Colle S. Giovanni (Viù, Turin, Piedmont), preserved in the Museum of the Institute of Systematic Zoology the University of Turin, shows no clear distinctive characters with respect to *A. pura*. Thus it was not possible to define the real status of this species. Fortunately field researches in the type locality of Pollonera's species yielded two living specimens for study of the structure of their genital tract. Unexpectedly '*Hyalinia*' *stabilei* could be confirmed as a good species, closely related to those belonging to genus *Retinella*.

In Switzerland, Mermod (1930) recorded *A. pura* in many localities. In his book (p. 58, Fig. 21) a drawing of the reproductive system shows the features of a *Retinella* or an *Oxychilus* (presence of a penial flagellum). Forcart (1957) suggests that Mermod's drawing is of the genital tract of *Oxychilus* (*Ortizius*) *clarus* (Held). Unfortunately it is not clear if Mermod's drawing of the radula (p. 59, Fig. 22) belongs to the same specimen. In this case the apparent absence of endocones on the first lateral teeth could be an indication that the specimen belongs to the genus *Retinella*. Nevertheless, in view of the lack of any reference to the collecting site of the dissected specimen, it is impossible to state to which of the many species and varieties listed as synonyms of *A. pura* it belongs.

Many 'species' are recorded for France. The oldest one is '*Helix*' *nitidosa* Férussac (1821, nomen nudum). Under this name, however, both Dupuy (1849) and Locard (1882, 1894) described several populations from north-east France, all more recently regarded as referable to *A. pura* (see Germain 1930, p. 58). Another species, '*Zonites*' *pilaticus*, was described by Bourguignat (1862) from material of M. Pilat (Monts du Lyonnais, Loire). This species, though considered a synonym of *A. pura* by Germain (1930), seems to differ both from Alder's species and from the two Italian *Retinella*, by the narrower umbilicus and the tightly coiled whorls (see Westerlund 1886, p. 43, Locard 1894, p. 59). Moreover Mermod (1930, p. 68, note), after having studied the type specimen, considered it to be based on a young specimen of *Oxychilus* (s.str.) *cellarius* (Müller). Precise information is lacking on '*Hyalinia*' *lenarrosta* Bourguignat in Locard (1894) from Estaing (Aveyron) and on '*Hyalinia*' *macralsobia* Bourguignat in Locard (1894) from the Forêt d'Orient (Aube), as well as on '*Zonites*' *udvaricus* sensu Locard (1894) (not Servain 1881) from Savoy. Their very brief descriptions are, in fact, insufficient for a clear understanding of their taxonomic status. In any case Germain (1930) regards them all as synonyms of *A. pura*.

Clearly it is impossible, at present, to revise all the different taxa listed above and to verify their real identities. We consider it reasonable, then, to maintain their assignment to Alder's species and to describe the two Italian *Retinella* as separate species. We hope that European colleagues will be encouraged by the present paper to revise anatomically all the populations of little Zonitidae resembling *A. pura*. Only in this way will it be possible to avoid incorrect identifications and perhaps to solve the problem of eventual synonymy.

### ***Retinella pseudoaegopinella* n.sp.**

#### *Description*

*Shell*: (Fig. 5A; Plate 14 A–B) fairly flat on top, thin and translucent, coloured with a more or less intense horny-olivaceous tinge, seldom whitish. Spire slightly raised, with 3 3/4–4 1/2 gently convexed whorls, rapidly increasing in width. Last whorl large, somewhat compressed, rounded and slightly widening near the aperture. Mouth oblique and oval, with a thin non everted lip. Moderately deep sutures. Umbilicus slightly eccentric, width



about 1/4 of the major diameter of the shell. External surface bright and polished, often more or less corroded at the apex or on the whorls, with faint growth lines which are more evident near the sutures and the mouth; a reticulated microsculpture is formed by the crossing of very delicate radial and spiral furrows (10–11 spiral lines on 100  $\mu\text{m}$  of the last whorl surface) (Plate 15 A–C). In the middle of the majority of the meshes of the reticulum the periostracal layer rises to form a tiny, somewhat wavy, comb (Plate 15C). On the protoconch the external surface shows evident spiral striae (Plate 15A).

*Height*: 1.9–2.1 mm; *major diameter*: 4.1–4.5 mm; *minor diameter*: 3.4–3.8 mm.

*The genital tract*: (Fig. 1 A–B) begins with the ovotestis which consist of three ovoid lobes. The gonoduct (= 1st hermaphrodite duct), slender where it originates from the gonad, is swollen in the middle, and grows thinner at the end before entering the talon (= fertilization chamber + receptaculum seminis complex). The talon leans against the albumen gland from the base of which the ovispermiduct (2nd hermaphrodite duct) begins. This last is wide but short, and is lobed in its female portion. The free oviduct is long and thickened before ending in the vagina. The bursa copulatrix (= gametolytic gland) has an elongated sac-like aspect; its duct (as long as the bursa) ends in the base of the vagina and has a characteristically S-shaped form. From the prostatic portion of the ovispermiduct originates a slender vas deferens. A long and thicker epiphallus follows the vas deferens. The epiphallus joins the penis defining a rather long penial flagellum at the apex of which the penial retractor muscle is inserted. The inner walls of the proximal part of the epiphallus show small papillae arranged in rows. These papillae in the distal part of the epiphallus merge to form longitudinal ridges (Fig. 3C). The penis is fairly short. Its distal portion is enveloped in a sheath connected to the distal portion of the epiphallus by slender bristles of connective tissue. The inner walls of the penis show a series of cristae. Two of these are larger and extend the entire penial length (Fig. 3C). The inner walls of the flagellum show ca. 10 rows of small papillae, arranged counter to the penial folds. The main five rows merge to form incontinuous wavy ridges, between which rows of isolated papillae are interposed. The penis and the vagina open side by side into a short genital atrium, with a narrow glandular external covering.

In a few specimens a long, thin, thread-like spermatophore with sharp ends was found in the bursa copulatrix (Fig. 1B).

*Jaw*: of oxygnathous type, arched, the inferior margin bearing a rather large central prominence faintly sharpened (Fig. 1C).

*The radula*: (Plate 17 A–C) shows many rows of 71–75 teeth each, disposed according to the formula:

$$\frac{31-32 \text{ M}}{1} + \frac{1-2 \text{ LM}}{2} + \frac{3 \text{ L}}{2} + \frac{\text{C}}{3} + \frac{3 \text{ L}}{2} + \frac{1-2 \text{ LM}}{2} + \frac{31-32 \text{ M}}{1}$$

The central tooth has a long and sharpened mesocone and short ectocones. The lateral teeth show a long mesocone and a small ectocone. The endocone is missing. One or two latero-marginal teeth are distinguished by the smaller basal plate, the long and curved mesocone and very small ectocone. There follows a row of 31–32 monocuspid marginal teeth, each with curved mesocone, gradually decreasing in dimensions towards the lateral margin of the radula.

Kidney and nervous system (Fig. 1 D–E) corresponding to those seen in the other *Retinella* species.

#### *Holotype*

‘Dolina di S. Lorenzo’, 1370 m, ‘Bosco di Rezzo’ (Rezzo, Imperia), A. Boato and M. Bodon leg. In Giusti collection (Institute of Zoology, University of Siena, Siena).

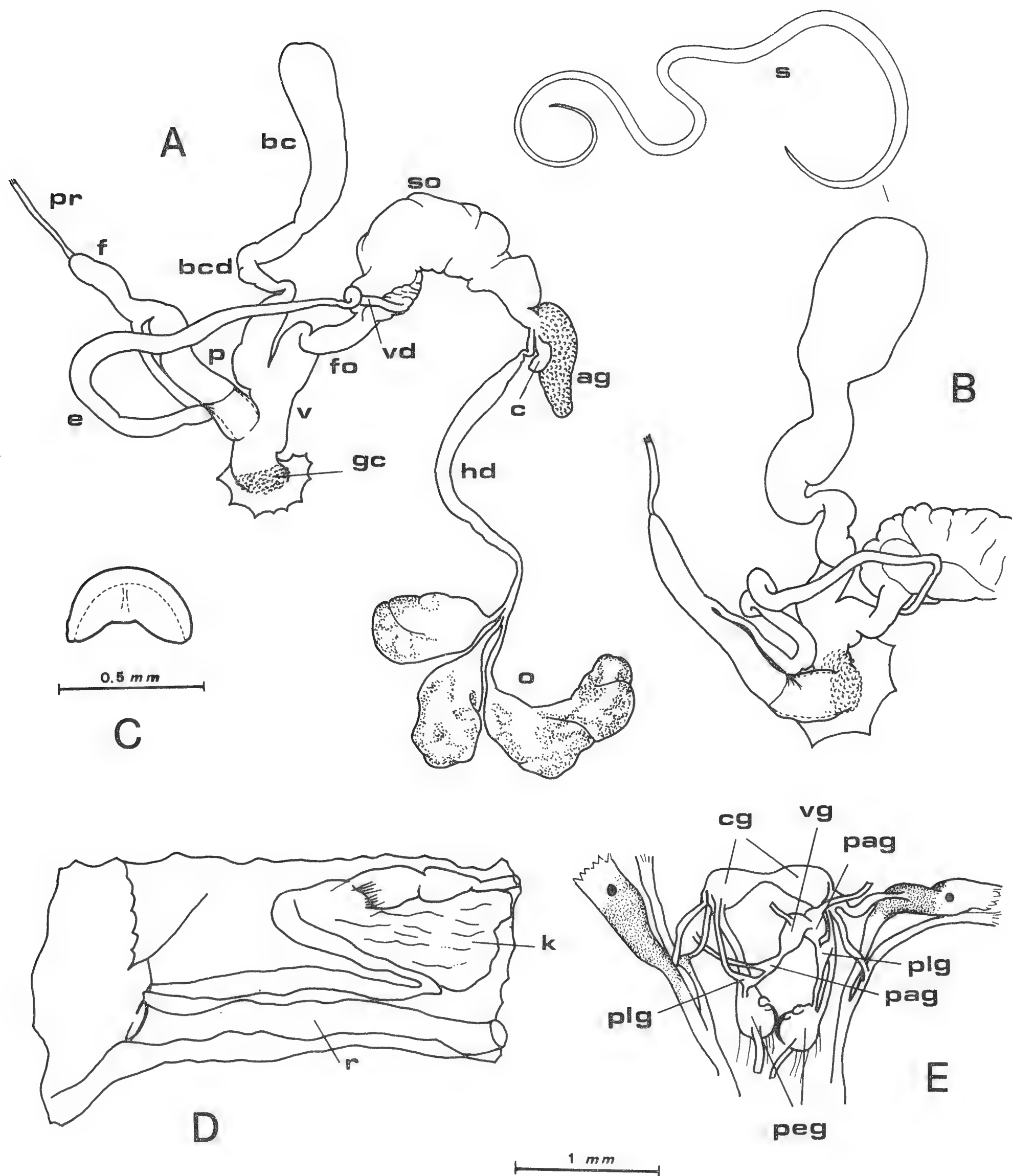


Fig. 1. *Retinella pseudoaegopinella* n.sp. A: Reproductive system (specimen from "Bosco di Rezzo", IM). B: Distal genitalia and a spermatophore, isolated from the bursa copulatrix (= gametolytic gland) (specimen from M. Fenera, VC). C, D, E: Jaw (C), internal view of pallial complex (D), nervous system (E) (specimens from 'Bosco di Rezzo', IM).

ag = albumen gland; bc = bursa copulatrix (= gametolytic gland); bcd = bursa copulatrix duct; c = claw (= talon); cg = cerebral ganglia; e = epiphallus; f = flagellum; fo = free oviduct; gc = glandular covering; hd = hermaphrodite duct; k = kidney; o = ovotestis; p = penis; pag = parietal ganglia; peg = pedal ganglia; plg = pleural ganglia; pr = penial retractor; r = rectum; s = spermatophore; so = sperm-oviduct; v = vagina; vd = vas deferens; vg = visceral ganglion.

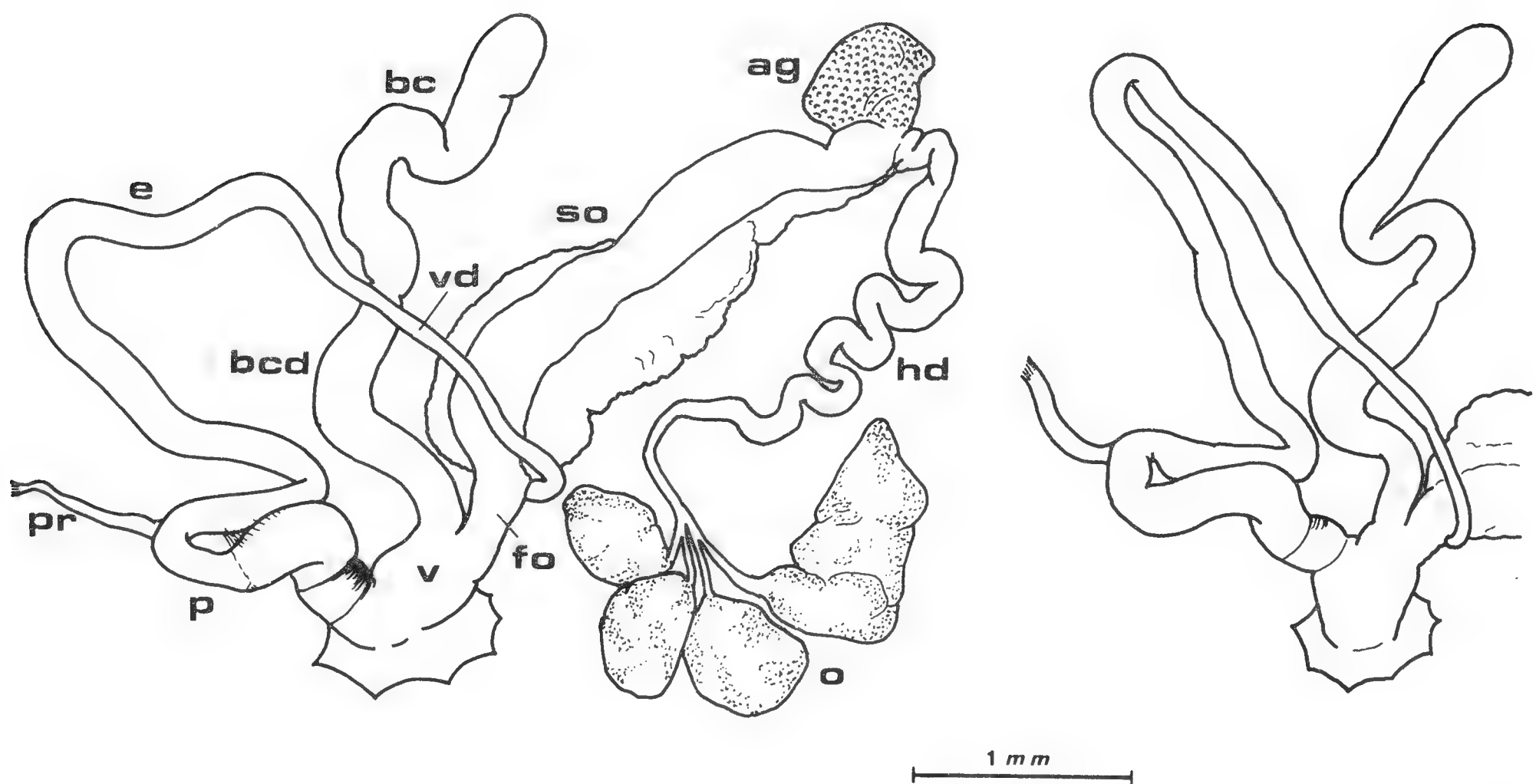


Fig. 2. *Retinella stabilei* (Pollonera). Reproductive system and distal genitalia (specimens from Colle S. Giovanni, TO).

ag = albumen gland; bc = bursa copulatrix; bcd = bursa copulatrix duct; e = epiphallus; fo = free oviduct; hd = hermaphrodite duct; o = ovotestis; p = penis; pr = penial retractor; so = sperm-oviduct; v = vagina; vd = vas deferens.

#### Paratypes

Ligurian Alps: 'Bosco di Rezzo', 1300–1600 m (Rezzo, IM), 18/6/77, 3 specimens; 12/9/81, 2 spec.; 31/10/81, 8 spec.; Melogno, 1220 m (Calizzano, SV), 24/10/81, 1 spec.; 'Fontana Meraviglie', M. Galero, 1190 m (Garessio, CN), 20/10/81, 4 spec.; 'Col di Tenda', 1700 m (Limone Piemonte, CN), 4/9/84, 4 spec. (Fig. 6).

Cottian Alps: Crissolo (Crissolo, CN), 29/7/84, 2 spec.; 30/7/84, 1 spec. (Fig. 6).

Pennine Alps: Near 'Grotta della Finestra', M. Fenera, 675 m (Valduggia, VC), 26/10/80, 1 spec. (Fig. 6).

In collection Giusti, Institute of Zoology, University of Siena; in collection Boato & Bodon, Institute of Zoology, University of Genoa.

#### Derivatio Nominis

The name *R. pseudoaegopinella* points out the close similarity between the shell of the new species and that of *A. pura*.

#### Discussion

The new species is clearly distinguished by the features of its genital tract from species belonging to the genus *Aegopinella* to which it could be referred by the shape, dimensions and microsculpture of the shell (Plates 15–16). It has some anatomical characters in common with the genus *Aegopinella*: the right tentacle retractor muscle running independently from the genital duct and the structure of the radula. However, it appears, in fact, to belong to the genus *Retinella* for the following characters (see Forcart 1957, 1960, 1965, Riedel 1980):

A) a penial flagellum on the apex of which the genital retractor muscle is inserted (Fig. 1 A–B).

B) a long epiphallus in which a spermatophore can be produced (Fig. 1 A–B).

Nevertheless the narrow glandular covering of the genital atrium seems to distinguish the new species from all the other *Retinella*. This structure is completely lacking among the characters included in the traditional descriptions of the genus (Forcart 1957, Riedel 1980).

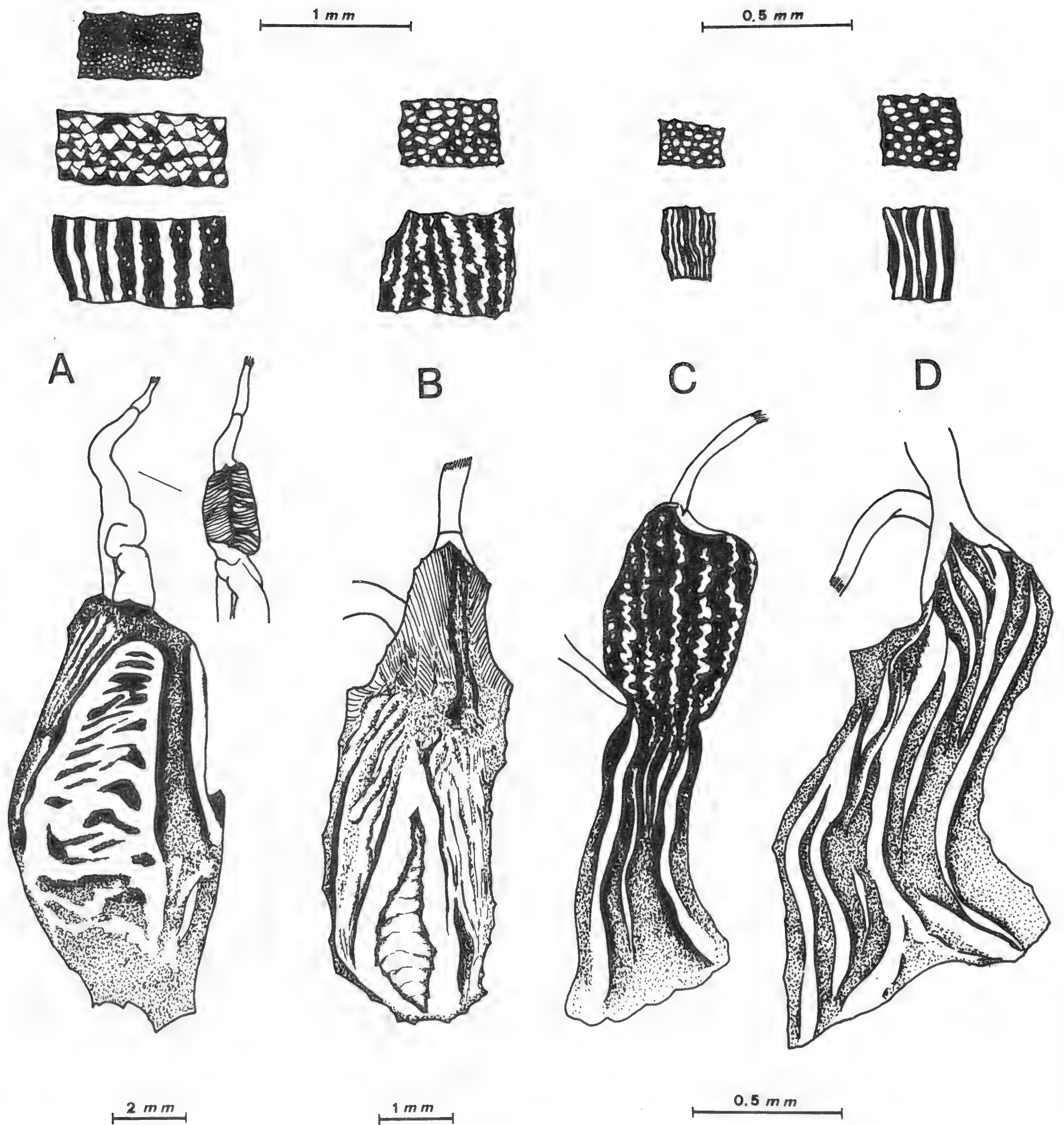


Fig. 3. Internal features of epiphallus, proximal to distal end (top), flagellum and penis (bottom) in *Retinella* spp.  
 A: *Retinella olivetorum* (Gmelin) specimens from M. Forato, LU (epiphallus), "Monte di Portofino", GE (flagellum and penis). B: *Retinella hiulca* (Albers) from Parlasco, CO. C: *Retinella pseudoaegopinella* n.sp. from M. Fenara, VC. D: *Retinella stabilei* (Pollonera) from Colle S. Giovanni, TO.



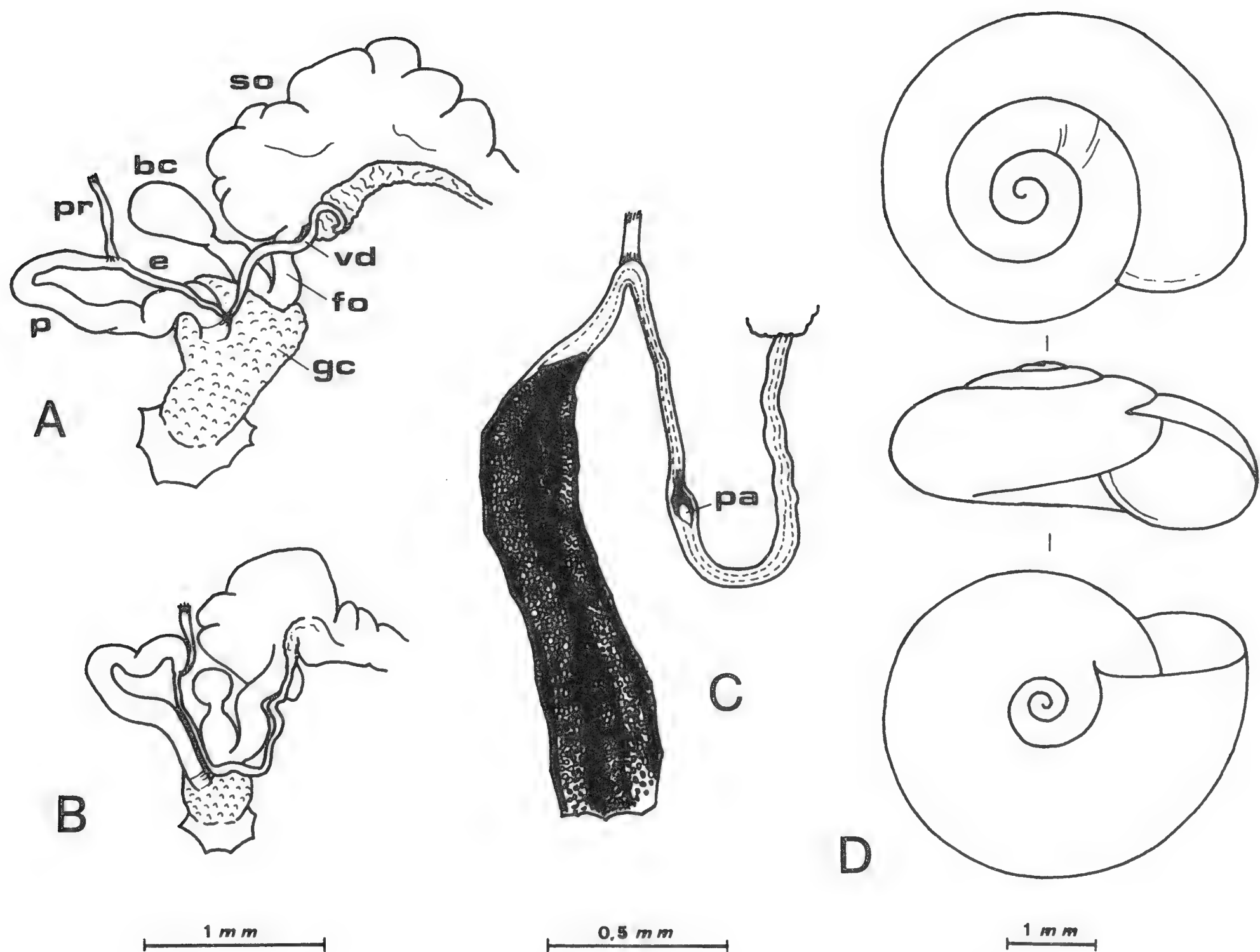


Fig. 4. *Aegopinella pura* (Alder). A–B: Distal genitalia (specimens from 'Passo di Romezzano', PR and "Foresta Umbra", FG). C: Internal features of penis and vas deferens (specimen from M. Corno, RI). D: Apical, frontal and umbilical outline of shell (specimen from "Passo di Romezzano", PR).

bc = bursa copulatrix; e = epiphallus; fo = free oviduct; gc = glandular covering; p = penis; pa = papilla; pr = penial retractor; so = sperm-oviduct; vd = vas deferens.

It is our opinion, at present, that erection of a new generic or subgeneric name is not warranted.

A group of N-American species, closely allied to the genus *Retinella* and once considered to belong to several subgenera of it, shows a vaginal or atrial glandular covering in its genital tract (a feature also present in a few species of the genus *Aegopinella*, e.g. *A. pura*; see Fig. 4 and also Forcart 1957). However these species, today included in the genus *Glyphyalinia* Von Martens, 1892 (Riedel 1980), bear differently sculptured shells and a set of different anatomical details: penis opening close to the genital atrium, above or coinciding with the glandular covering; penial flagellum at times lacking, if present, more or less developed but very often independent of the penial retractor; epiphallus almost as wide as the penis, vagina completely enveloped by a glandular covering (see Pilsbry 1946, Riedel 1980).

With the exception of the atrial gland, all the other characters suggest the inclusion of *R. pseudoaegopinella* n.sp. in the subgenus *Retinella* (s. str.). However, as indicated in our concluding remarks, the different species of *Retinella* show such a great variability in the characters of their genital tract and shell that it is to be questioned whether the extant subgenera correspond to natural groupings. We therefore prefer to avoid the use of a subgeneric name in our description.

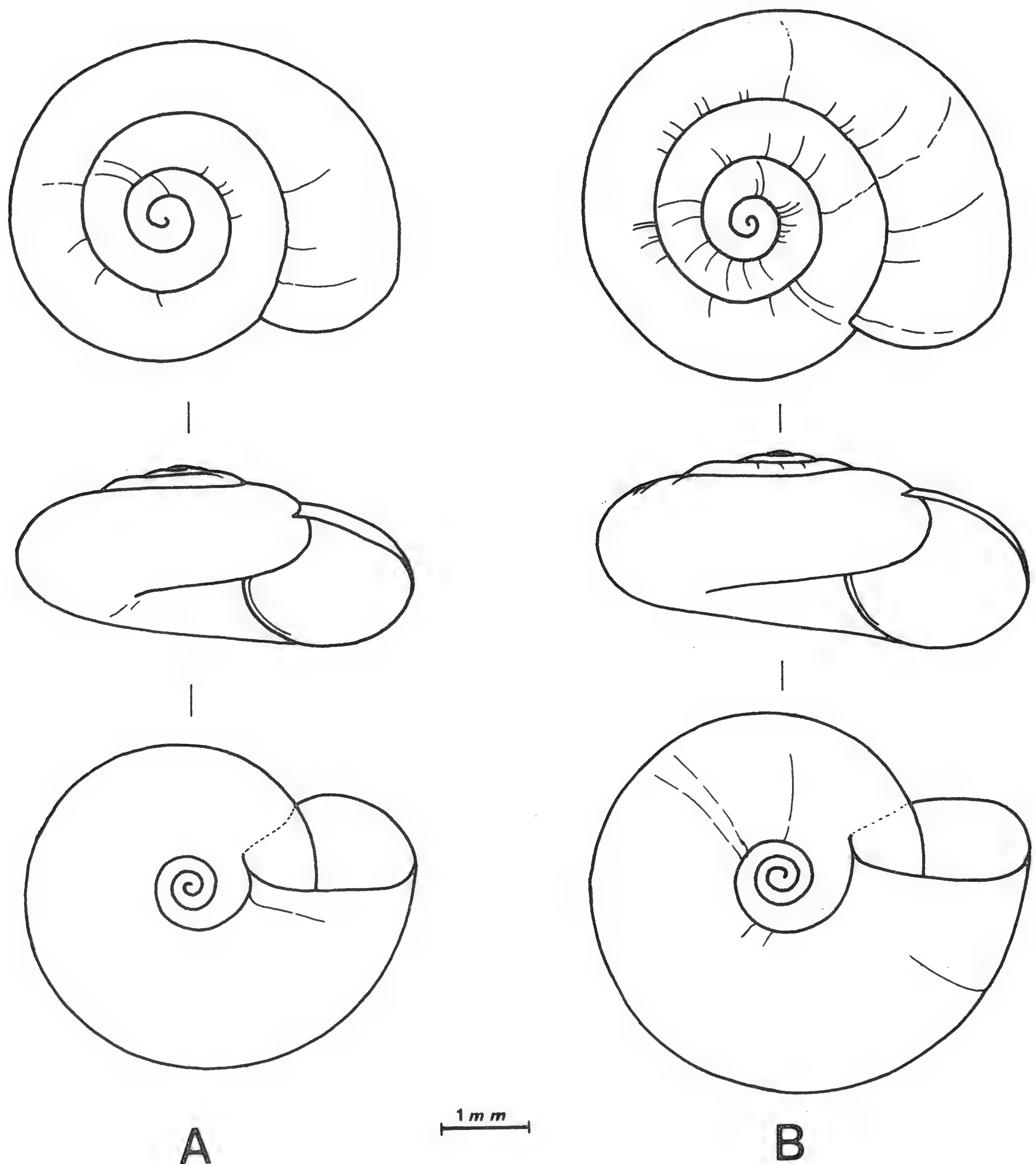


Fig. 5. *Retinella pseudoaegopinella* n.sp. (A) and *Retinella stabilei* (Pollonera) (B). Apical, frontal and umbilical outline of shells. (A: specimen from 'Bosco di Rezzo', IM; B: specimen from Colle S. Giovanni, TO).

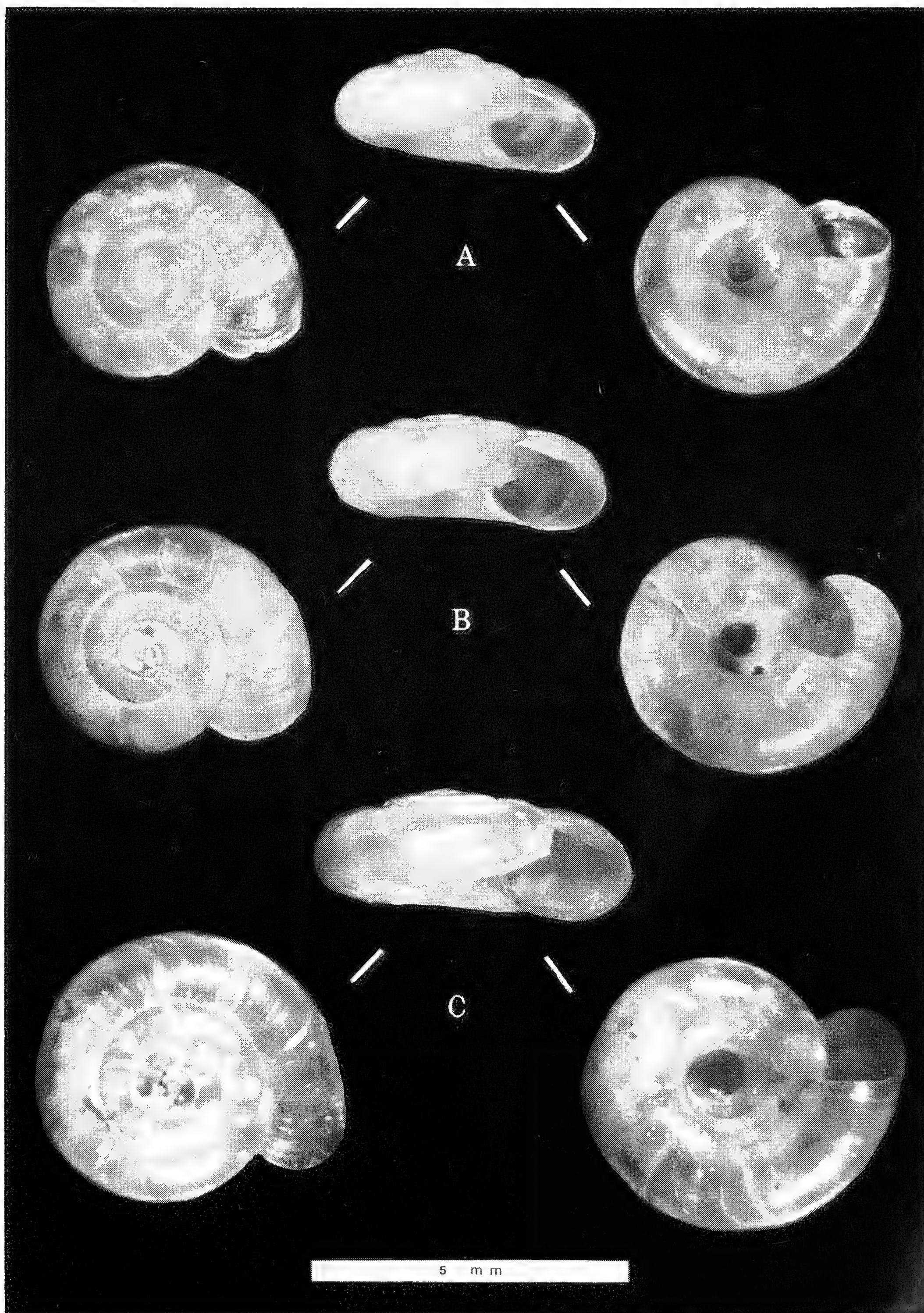
PLATE 14 (opposite)

Type (A) and paratype (B) of *Retinella pseudoaegopinella* n.sp. from "Bosco di Rezzo", IM and lectotype (C) of *Retinella stabilei* (Pollonera) from Colle S. Giovanni, TO.

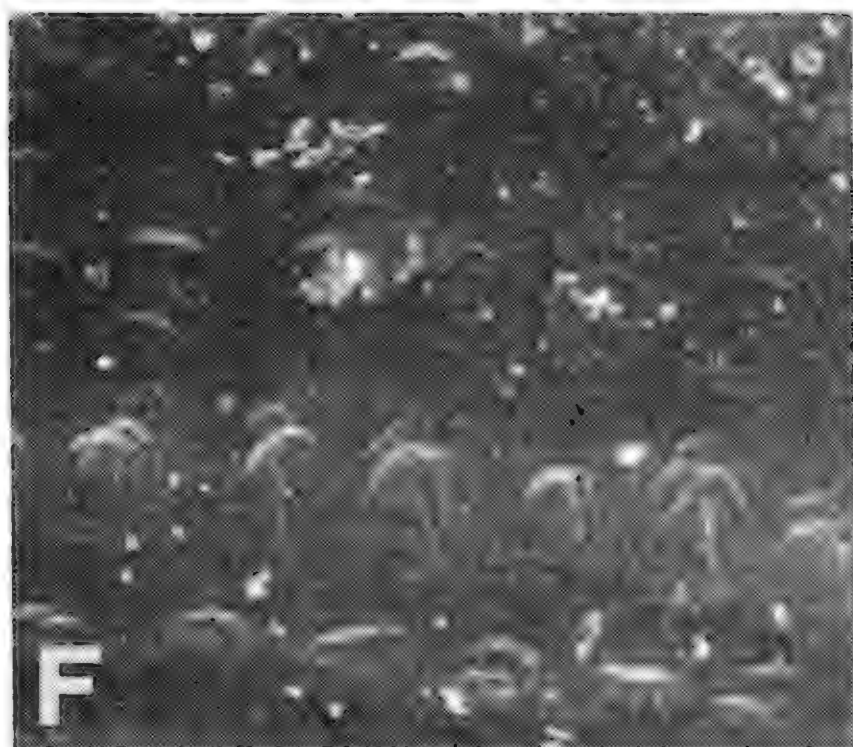
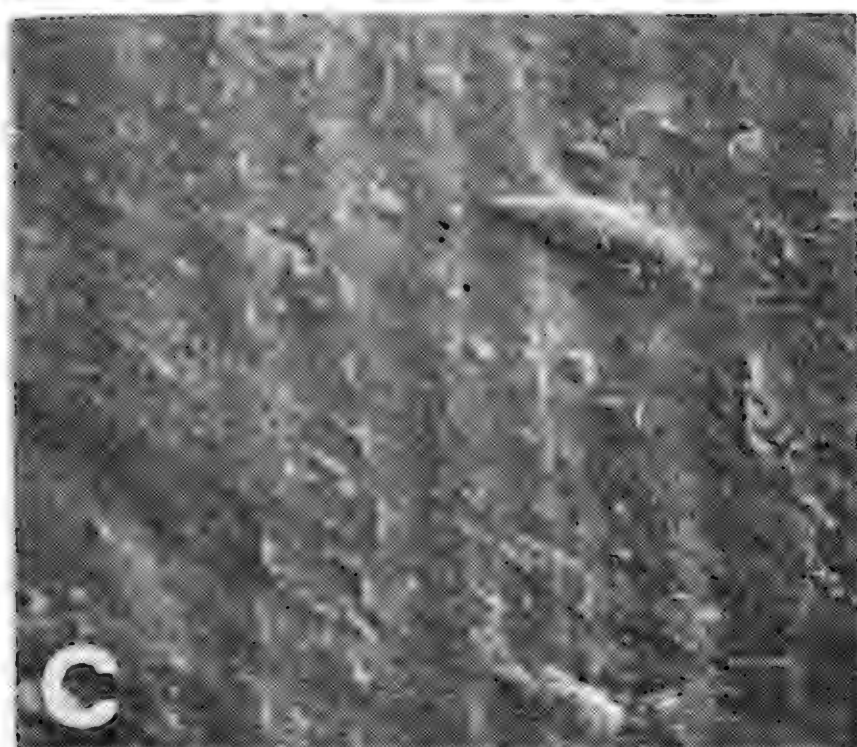
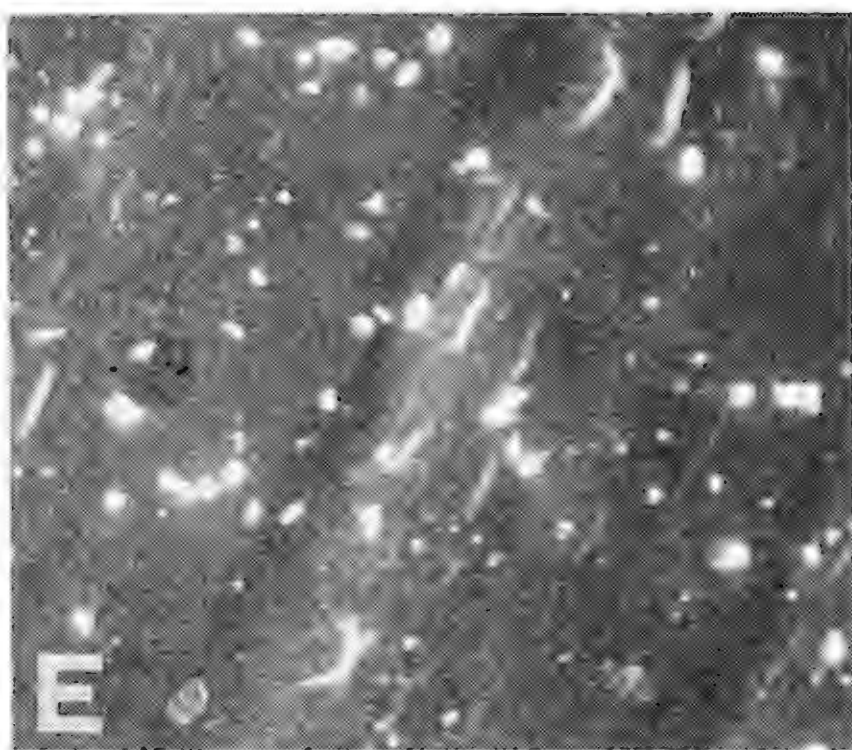
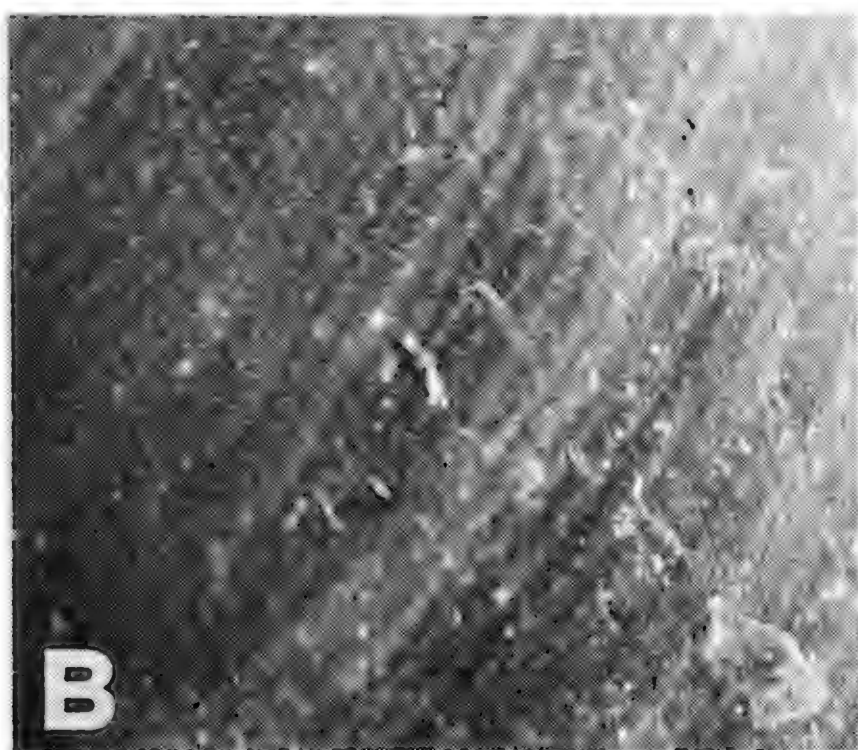
PLATE 15 (overleaf)

External shell surface of *Retinella pseudoaegopinella* n.sp. (A–C) and of *Retinella stabilei* (Pollonera) (D–F). A: The surface of the protoconch (P) shows spiral striae, while that of the first whorl (1) shows a reticulated microsculpture (300 X). B–C: The surface of the shell at different magnification (B: 300 X; C: 1000 X). Note the reticulated microsculpture and in the middle of the majority of the meshes of the reticulum the periostracal layer which rises to form tiny combs (arrows). D–F: Different zones of the shell surface. Note the reticulated structure and, in coincidence with the meshes of the reticulum, the periostracum which rises to form a simple comb or series of combs sometimes fused to form star-like structures (1000 X).











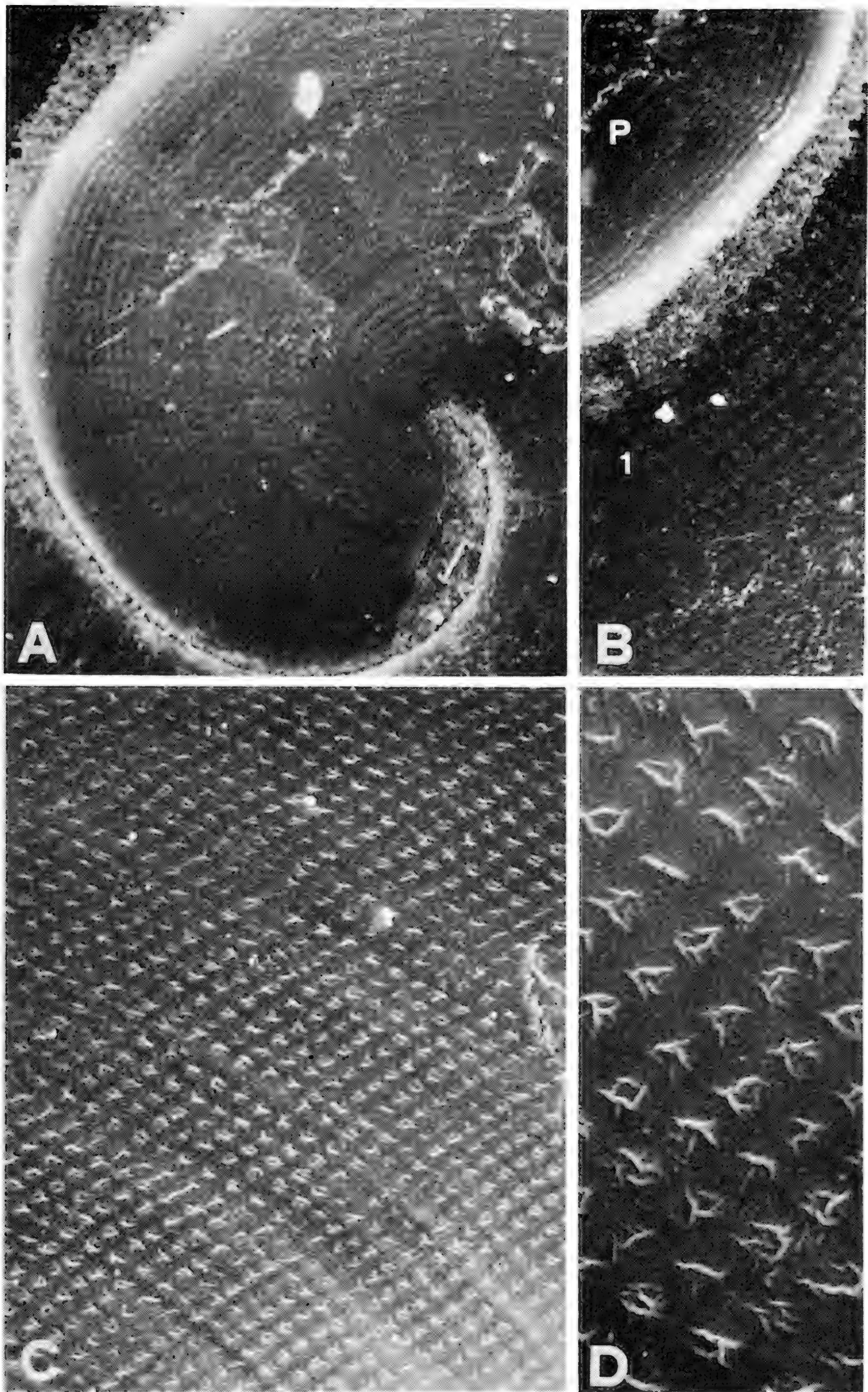


PLATE 16

External shell surface of *Aegopinella pura* (Alder) (specimen from Reatini Mountains, Central Apennines). A–B: The protoconch (P) shows spiral striae on its surface while the first whorl (1) has a reticulated microsculpture (300 X). C–D: The surface of the last whorl has a reticulated microsculpture. In the middle of each mesh of the reticulum the periostracum rises to form star-like structures or, infrequently, simple combs (C: 500 X; D: 1000 X).



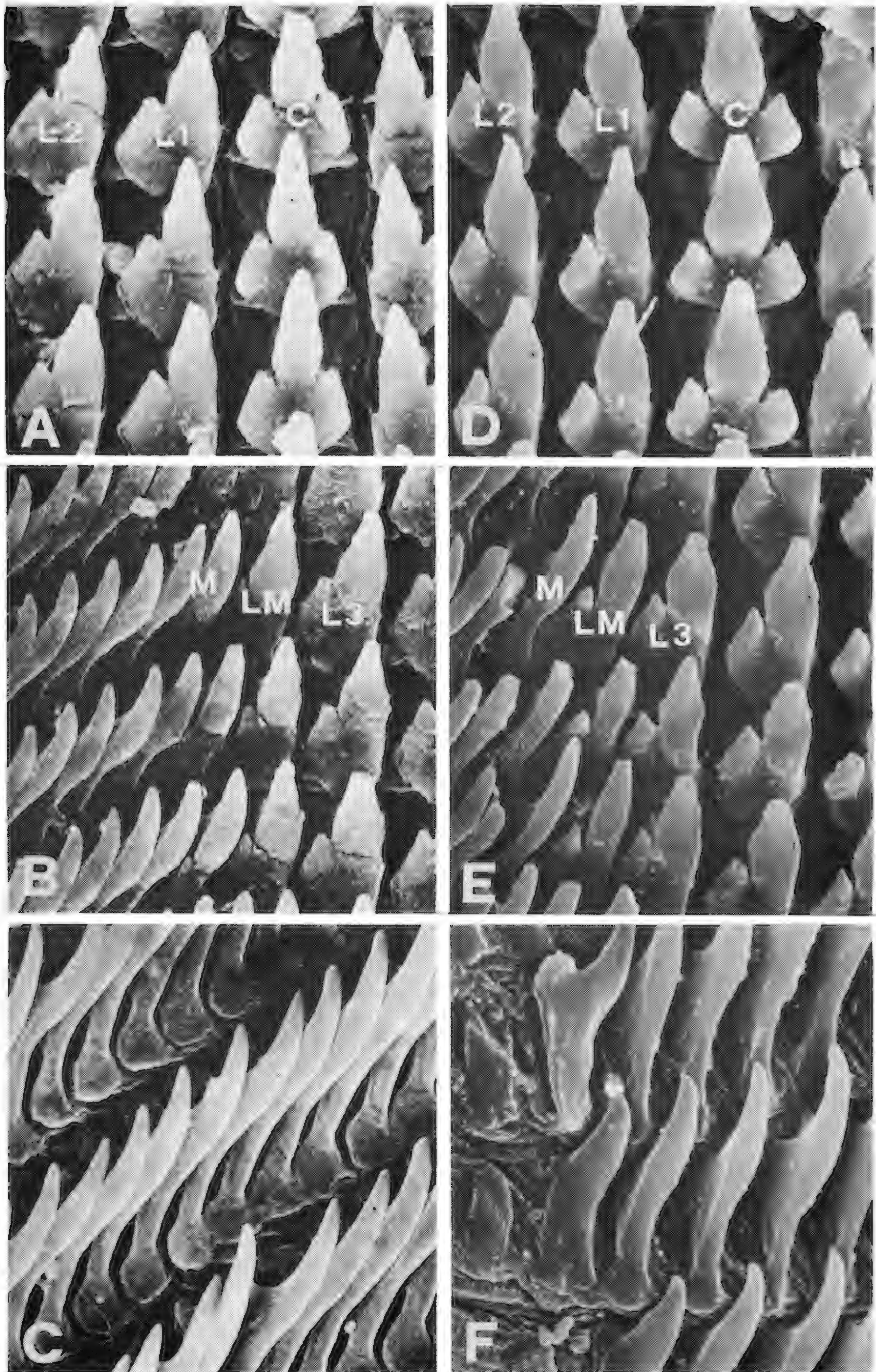


PLATE 17

Different portions of the radula of *Retinella pseudoaegopinella* n.sp. (A-C) and of *Retinella stabilei* (Pollonera) (D-F). A, D: Central portion of the radula; C = central (= rachidial) tooth; L1, L2 = first and second lateral teeth (1000 X). B, E: Lateral portion of the radula; L3 = third lateral tooth; LM = latero- marginal tooth; M = marginal teeth (1000 X). C: Marginal teeth (1500 X). F: Extreme marginal teeth (1000 X).



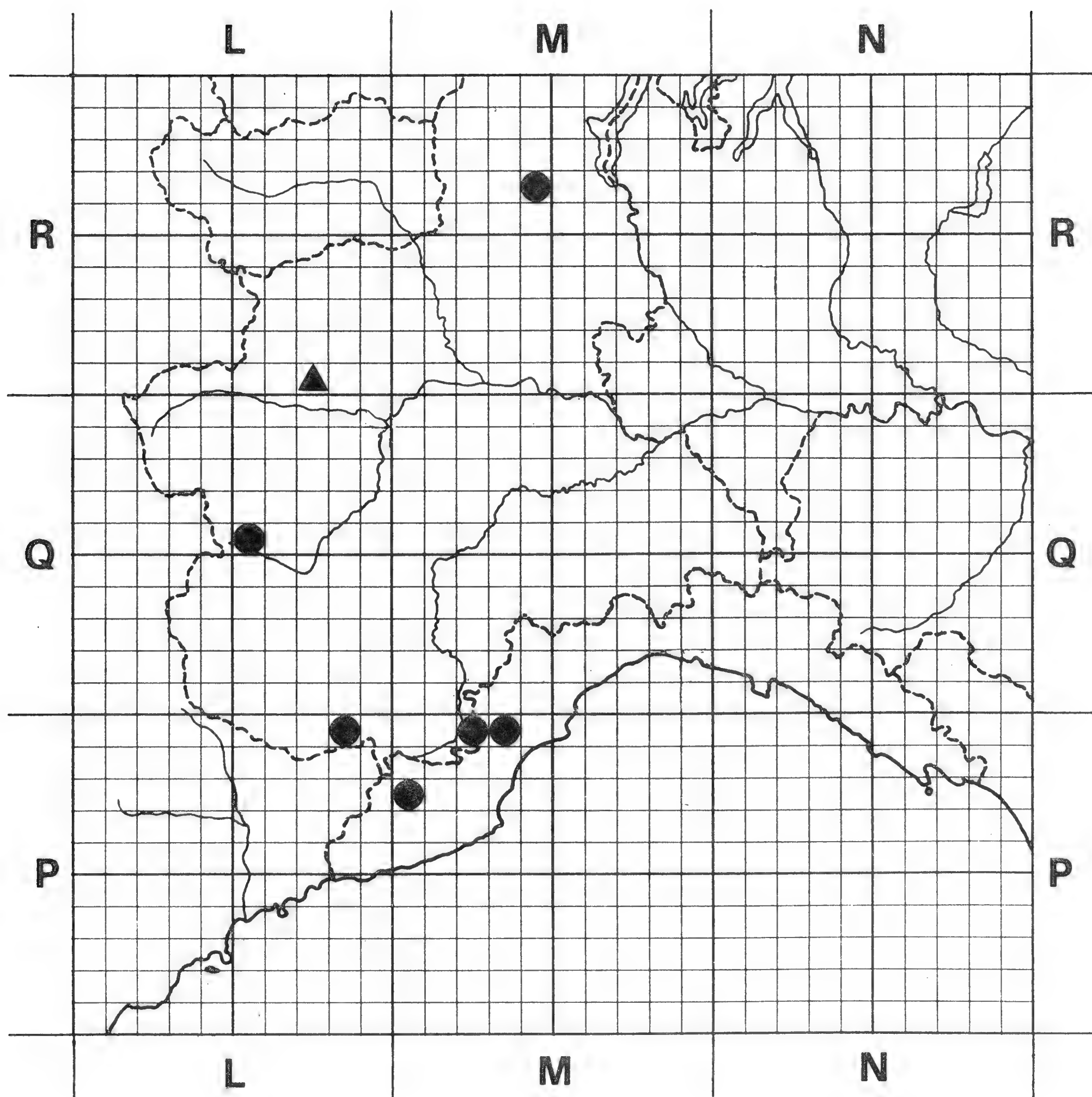


Fig. 6. Registered distribution of *Retinella pseudoaegopinella* n.sp. (black circles) and *Retinella stabilei* (Pollonera) (black triangle) and UTM notation of  $10 \times 10$  Kms squares.

Among the species usually considered as belonging to the subgenus *Retinella* (s.str.), *R. hiulca* (Albers) is that most similar to *R. pseudoaegopinella* n.sp., *R. hiulca*, however, besides the larger and globular shell (major diameter attaining 1.2–1.5 cm) shows a reduced vagina which lacks any glandular covering and a smaller bursa copulatrix which has a longer duct. No confusion is possible, with the species usually included in the subgenera *Retinelloides* Riedel and *Lyrodiscus* Pilsbry, because of the remarkable anatomical differences and also the peculiar shell structure and the sculpture of its external surface. In the first case, in fact, the shell appears to be globular, with regularly increasing whorls, the last of which is not enlarged, and with a roundish mouth. In the second case, the shell is characterized by slowly increasing whorls and strong, regularly spaced ribs on the external shell surface (see Germain 1930, Riedel 1980).

*Retinella pseudoaegopinella* n.sp. inhabits the litter of deciduous forest in shaded areas. Its presence seems to be independent of the chemical composition of the substratum. It is frequently associated with species of the genera *Pagodulina*, *Punctum*, *Discus*, *Vitrea*, etc.

### ***Retinella stabilei* (Pollonera)**

- Hyalinia (Polita) stabilei* Pollonera, 1886, Boll. Mus. Zool. Anat. Comp. R. Univ. Torino, 1 (17), p. 2. Locus typicus restrictus: Colle di S. Giovanni, 1154 m, Valle Stura di Lanzo.  
*Hyalinia mixta* Pollonera, 1889 (not Westerlund 1886), Boll. Mus. Zool. Anat. Comp. R. Univ. Torino, 4 (58), pp. 2–3.  
*Hyalinia (Polita) mixta* Westerlund, 1890 (not Westerlund 1886), Fauna, Suppl. 1, p. 5.  
*Retinella (Aegopinella) pura mixta* partim, Alzona, 1971 (not Westerlund 1886), Atti Soc. It. Sc. Nat. Mus. Civ. St. Nat. Milano, 111, p. 122.

#### *Description*

*Shell*: (Fig. 5B; Plate 14C) depressed, almost flat on top, thin, translucent, horny-coloured. Spire with 4 1/2 rapidly increasing whorls; last whorl widened and round. Oblique, oval mouth; thin lip, not everted. Moderately deep sutures. Umbilicus slightly eccentric, width 1/4 of the major diameter of the shell. External surface bright and polished, with faint growth lines which are more evident near the sutures; a reticulated microsculpture is formed by the crossing of very delicate radial and spiral furrows (11–12 spiral lines on 100  $\mu$ m of the last whorl surface (Plate 15 D–E). In the middle of each mesh of the reticulum the periostracal layer rises to form little ridges, infrequently with some branching (Plate 15 E–F).

*Height*: 2.0–2.3 mm; major diameter: 4.8–5.3 mm; minor diameter: 4.1–4.6 mm.

*The reproductive genital tract*: (Fig. 2) begins with the ovotestis which consist of 4–5 ovoid lobes. The gonoduct (= 1st hermaphrodite duct) is slender as it takes origin from the gonad, swollen and bent in the middle and grows thinner at the end, before entering the talon (= fertilization chamber + receptaculum seminis complex). The talon lies against the albumen gland at the base of which the ovispermiduct (= 2nd hermaphrodite duct) begins. The latter is wide but short and is lobed in its female portion. The short free oviduct leads to a short and wide vagina. The bursa copulatrix (= gametolytic gland) has an elongated S-like shape; its duct is wide and fairly long. From the prostatic portion of the ovispermiduct originates a slender and short vas deferens. The vas deferens continues in a wider and long canal which can be interpreted as an epiphallus. This last, in its turn, continues in the penis, the beginning of which can be defined by the insertion of the penial retractor muscle. There is no evidence at all of a penial flagellum. Internally the epiphallus (Fig. 3D) shows small papillae in its proximal part. These papillae merge in the distal portion of the epiphallus to form 4–5 longitudinal ridges. The rather short and swollen penis is enveloped in a sheath which is joined by connective tissue strands to the distal curve of the epiphallus. The internal surface of the penis walls shows, over its entire length, 5–8 ridges of variable dimensions (Fig. 3D). The penis and vagina open side by side into a short genital atrium. The external surface of the atrium lacks a glandular covering.

*Jaw*: of oxygnathous type, curved, the inferior margin bearing a short central prominence.

*The radula*: (Plate 17 D–F) shows many rows of 57–61 teeth, arranged according to the formula:

$$\frac{23-25 \text{ M}}{1} + \frac{1-2 \text{ LM}}{2} + \frac{3 \text{ L}}{2} + \frac{\text{C}}{3} + \frac{3 \text{ L}}{2} + \frac{1-2 \text{ LM}}{2} + \frac{23-25 \text{ M}}{1}$$



The central tooth is rather large and shows a long and sharpened mesocone and two small sharpened ectocones. The lateral teeth, three on each side, have a mesocone and only a small ectocone. The latero-marginal teeth are characterized by a reduced basal plate and a curved mesocone flanked by a small ectocone. The 23–25 lateral teeth have a simple sharp point and dimensions decreasing towards the lateral margins of the radula.

#### *Lectotype*

We have chosen as lectotype (Plate 14C) the shell named '*Hyalinia stabilei*', deposited in the Pollonera collection (Museum of Systematic Zoology, University of Turin), collected in the first of the two localities listed by Pollonera (1886): Colle S. Giovanni, Valle Stura di Lanzo, Torino (locus typicus restrictus!) (Fig. 6).

Another shell, preserved in a separate tube and collected near Courmayeur, Val d'Aosta (the second collecting site listed by Pollonera 1886) cannot be, at present, elected as paralectotype. In fact, even if it is very similar to the lectotype, no information is available on the soft parts of corresponding living specimens.

*Other material examined*: two specimens collected on the 'Colle S. Giovanni' (Viù, Turin), 7/11/83.

#### *Discussion*

*Retinella stabilei* (Pollonera) although very similar in shell shape to *Retinella pseudoaegopinella* n.sp. and to *Aegopinella pura* (Alder) (Figs. 4–5; Plate 14) is clearly distinguishable from both species thanks to evident anatomical differences. The lack of a penial flagellum and of a glandular covering of the genital atrium walls are diagnostic features with respect to *R. pseudoaegopinella* n.sp. For such features *R. stabilei* (Pollonera) approaches *R. (Retinelloides) incerta* (Draparnaud) from the Pyrenees. Nevertheless the latter species is characterized by a larger and more globular shell ( $h = 9\text{--}12$  mm; major diameter = 15–20 mm). Moreover *R. (Retinelloides) incerta* shows a longer ductus of the bursa copulatrix, a pear-shaped bursa copulatrix, a shorter epiphallus and an evident penial papilla placed where the epiphallus opens into the penis. This last feature is completely lacking in *R. stabilei*. This prevents *R. stabilei* from being included in the subgenus *Retinelloides* with *R. incerta* (see concluding remarks).

The internal structure of the male portion of the genital tract allows a clear distinction between *R. stabilei* and *Aegopinella pura*. In fact, *A. pura* shows an evident papilla (Fig. 4C) where the vas deferens opens into a duct which could be interpreted as the 'epiphallus'. (Riedel (1980) regards this duct as a portion of the vas deferens.) Thus the genus *Aegopinella* would be distinguished by the lack of an epiphallus. This opinion seems to be confirmed by the fact that spermatophores are not produced in the different species of the genus (Forcart, 1957, talks about sperm masses). This 'epiphallus' has a reduced diameter and ends in the penis just where the penial retractor is inserted (Fig. 4 A–B). The internal walls of the penis show two longitudinal ridges and a surface covered by minute papillae (Fig. 4C). As already stated, *R. stabilei* lacks a papilla both at the end of its vas deferens and in its epiphallus. Moreover the inner surface of epiphallus walls is very similar to that of the typus generis *R. olivetorum* (Gmelin) (Fig. 3).

*R. stabilei* (Pollonera) lives in the litter. It has been collected in moist, shaded sites in mountain woodlands on non-calcareous soils.

#### CONCLUDING REMARKS

The identification of the two above-described *Retinella* is very interesting from both biogeographical and taxonomical points of view. First of all, the present paper indicates the

presence in Europe of species that can be easily confused with *Aegopinella pura* (Alder), thus suggesting that a thorough revision, based on anatomical research, of the populations which have been more or less recently assigned to Alder's species is necessary. Second, our findings increase the number of species belonging to a genus, *Retinella*, which is known only in European and N-African regions but which shows strong relations to some genera of the N-American malacofauna. Therefore it can be hypothesized that these genera descend from a common laurasiatic ancestral group that in our opinion may be traced to the late Mesozoic (to Oligocene according to Forcart 1957).

Moreover the present subdivision in subgenera of the genus *Retinella* now appears to be rather questionable. According to Riedel (1980), in fact, three subgenera, all lacking a vaginal gland, would belong to the genus *Retinella*:

*Retinella* (s.str.) is distinguished by:

- A) a penial flagellum at the apex of which the penial retractor is inserted;
- B) an epiphallus opening on a side of the penis;
- C) the absence of a penial papilla.

*Retinelloides* Riedel, 1980, distinguished by:

- A) the lack of a penial flagellum;
- B) the penial retractor inserted where the epiphallus ends and the penis begins.
- C) a penial papilla is present where the epiphallus opens into the penis.

*Lyrodiscus* Pilsbry, 1893, endemic of the Canary Islands, anatomically rather similar to *Retinella* (s.str.), characterized by:

- A) pronounced spiral ribs on the external surface of the shell whorls.

The two *Retinella* discussed here cannot be assigned to one of these subgenera. In fact, *R. pseudoaegopinella* n.sp. shows a genital tract closely similar to that of species belonging to *Retinella* (s.str.) but is provided with a glandular ring covering the walls of the genital atrium just as in some of the nearctic species of the genus *Glyphyalinia* Von Martens, 1892. As previously observed these species lack a penial flagellum or show a differently shaped one.

*Retinella stabilei* (Pollonera), on the other hand, lacks a glandular covering as well as a penial flagellum just like the single species of the subgenus *Retinelloides*. Nevertheless *R. stabilei* is differentiated from *R. (Retinelloides) incerta* by its lack of a penial papilla placed where the epiphallus opens into the penis.

Moreover the two species herein described have almost identical shells, (with respect to *R. pseudoaegopinella* n.sp., *R. stabilei* seems only to differ by the slightly narrower last whorl and the slightly larger size.) with a microsculpture very similar to that of *Aegopinella pura* (Plates 15–16), while the shells of *Retinella* (s.str.) and *Retinelloides* show no evident microsculpture, and those of *Lyrodiscus* a quite different one. In addition, the two species *R. pseudoaegopinella* n.sp. and *R. stabilei* (Pollonera) are clearly distinguishable by their small size from the other congeneric species, *R. olivetorum* (Gmelin 1789), *R. hiulca* (Albers 1850), *R. tetuanensis* (Kobelt 1881) and *R. incerta* (Draparnaud 1805).

Thus it is evident that the various species which at present can be interpreted as belonging to the genus *Retinella* are distinguished from one another by different combinations of the same characters. In such a situation it is impossible not only to identify the real limits of the subgenera (perhaps with the exception of *Lyrodiscus*) but also to identify a boundary line between *Retinella* and other taxa such as the N-American genus *Glyphyalinia*. In view of the lack of more reliable information on the relationships among the various species of *Retinella* we prefer to abstain from using a subgeneric subdivision and simply to regard *Retinella* as a very polymorphous taxon. In fact, in our opinion, it does not seem advisable to increase the number of generic or subgeneric subdivisions whenever a species disagrees for only one or a few characters whose adaptive significance is not clear.

## ACKNOWLEDGMENTS

We would like to express our thanks to Dr. G. Andersson of the Göteborg Museum and to Prof. U. Parenti Director of the Syst. Zool. Inst., the University of Turin, for having loaned us the type material of *Hyalinia stabilei* and '*Hyalinia*' *mixta*. and to Dr. A. Riedel of Warsaw (Poland) who kindly surveyed our data; his conclusive remarks (in litt.) are completely in agreement with ours.

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## A NEW SPECIES OF *MURICOPSIS* FROM OMAN (PROSOBRANCHIA: MURICACEA)

KATHLEEN R. SMYTHE<sup>1</sup> AND P. GRAHAM OLIVER<sup>2</sup>

(Accepted for publication, 19th October 1985)

**Abstract:** A new species of *Muricopsis* (*M. omanensis* n. sp.) is described from the areas of Masirah and Dhofar, Oman. This species is most clearly allied to the Mediterranean *M. blainvillei* (Payraudeau). The two are differentiated on characters of colour, shape, sculpture and aperture. To date *M. omanensis* is known only from the Masirah and Dhofar areas, and is probably part of a restricted fauna influenced by cold upwelling currents which typify the oceanography of that region.

### INTRODUCTION

This species first came to the attention of one of the authors (KRS) when on a shell collecting trip to Masirah Island in the company of Dr. Donald T. Bosch and family in December 1980. Subsequently, the other author (PGO) found the radula and tentatively placed it in the genus *Muricopsis*. The generic definitions of the smaller muricids and thaidids are poor, and based primarily on shell characters which may or may not reflect major anatomical differences. Radular characters are infrequently cited but here again the variation in the dentition may not reflect phylogeny but rather some ecological parameter. Consequently, the identity and relationships of this species could only be arrived at after checking all the literature on the Erythraean, Arabian, Indian Ocean, Indo-Pacific and Mediterranean faunas. Surveys of the major taxonomic works on the Muricacea (Radwin & d'Attilio 1976, Fair 1976 and Vokes 1971) yielded no identical species and neither did a search of the collections of the British Museum (Natural History) and the National Museum of Wales. Consequently this species is described as new.

***Muricopsis*** Bucquoy and Dautzenberg, 1882  
Type species: ***Murex blainvillei*** Payraudeau, 1826  
***Muricopsis omanensis*** n. sp.

#### *Type material*

**Holotype:** NMW.Z.1985.043.1. Jazirat Shinzi, Masirah Island, 20°34'N 50°58'E. Coll. K. R. Smythe. Height 27.05, breadth 12.45, aperture including canal 14.1 mm.

**Paratypes:** NMW.Z.1985.043.2,3. 2 specimens; NMW.Z.1985.043.4. S.E.M. mount of radula; BM(NH) 198096; ONHM 1984/69E all Jazirat Shinzi: Masirah Island: BM(NH) 1985097 Wadi Haart, Dhofar, coll. J. D. Taylor. Other paratypes currently in the collections of K. R. Smythe and D. T. Bosch to be lodged in the Oman Natural History Museum, the Zoological Museum, Amsterdam and the Smithsonian Institution, Washington.

<sup>1</sup> 6 Blondell Drive, Bognor Regis, PO21 4BQ.

<sup>2</sup> National Museum of Wales, Cathays Park, Cardiff, CF1 3NP.

*Description*

*Teleoconch* (Plate 18, Figs. 1a,b): fusiform, moderately elongated, approximately twice as high as broad with a short tapering spire and a short siphonal canal. The body whorl comprises on average 66% of the height. The average sizes of a random sample of 10 shells were: height 24.5 mm, width 11.5 mm and aperture including siphonal canal 13 mm. The sutures are impressed but not deeply incised. Apart from the protoconch and body whorl there are four to five spire whorls.

Sculpture of axial ribs crossed by spiral ridges and inter ridge lines (Plate 19, Fig. 2a), these being crossed by fine lamellar axial striae which if not worn produce scales on the spiral sculpture (Plate 19, Fig. 2b). Over the whole of the teleoconch there is a microscopic sculpture of spiral lines (Plate 19, Fig. 2b). On all whorls there are 7–9, usually 8 axial ribs. On the body whorl there are 8–9 spiral ridges each with between 3–5 inter ridge lines, on the other whorls there are only 3–4 spiral ridges. On all whorls the spiral ridges are thickened where they cross the axial ribs.

*Protoconch* (Plate 19, Fig. 2c): of  $1\frac{1}{2}$  whorls, smooth, tabulate.

*Aperture* (Plate 18, Fig. 1b): oval, approximately 50% of the height with a short siphonal canal which is inclined to the left and recurved dorsally at the tip. The outer lip has 5–6 small denticles within, usually 5 in which case there is one near to the weak anal sulcus and the other 4 closer together near the anterior, if the 6th is present it is very small and fills the gap. In juvenile shells there are no apertural denticles. The columella is extended from the body whorl for the greater part in the form of a thin lamellar ridge which forms a small pseudoumbilicus. There are 1–2 small columella folds close to the anterior end.

*Colour*: most shells are heavily encrusted such that the colour and sculpture are totally obscured. In clean shells the colour pattern is striking, the background being a rich mahogany-brown contrasting with the darker spiral lines and ridges of which the latter are purple-brown to black where they cross the axial ribs. The aperture is glossy and varies from a pale lilac to a deeper violet.

*Operculum* (Plate 19, Fig. 2d): oval, moderately thick, labial half thicker than parietal, somewhat depressed centrally.

*Radula* (Plate 19, Figs. 2e, f): rachiglossan, lateral teeth simple sickle shaped. Rachidian tooth with a large central cusp and smaller lateral cusps. (See Plate 19, and Figs. 1e and 1f). Between the lateral cusp and the basal endpoint are three denticles.

In the living animal the sole of the foot is cream, the upper part of the body a mottled dark purplish-brown. The tentacles are long, slender, purple brown in colour except for the white tips. The siphon is white.

*Habitat*

This species inhabits cracks and crevices in low cliffs or larger rocky outcrops from the mid tide level down. It appears to prefer sheltered areas as opposed to *Sinistralia gallagheri* Smythe and Chatfield (1981) which lives on or under rocks in exposed regions. *M. omanensis* further contrasts with another intertidal muricid *Farvartia paulboschi* Houart and Smythe (1984) which prefers the undersides of soft limestone slabs in areas of high silt content.

*Distribution*

Known only from Jazirat Shinzi and Ras Shagaaf on the east and west coasts of Masirah respectively and from Wadi Haart, near Sudh, and other areas near Mirbat, Dhofar, the southern province of Oman. This distribution although greatly restricted coincides with an area of cold upwelling currents close to the shore. This is yet another species apparently unique to these areas as discussed by Taylor and Smythe (1985).



1a



1b



PLATE 18

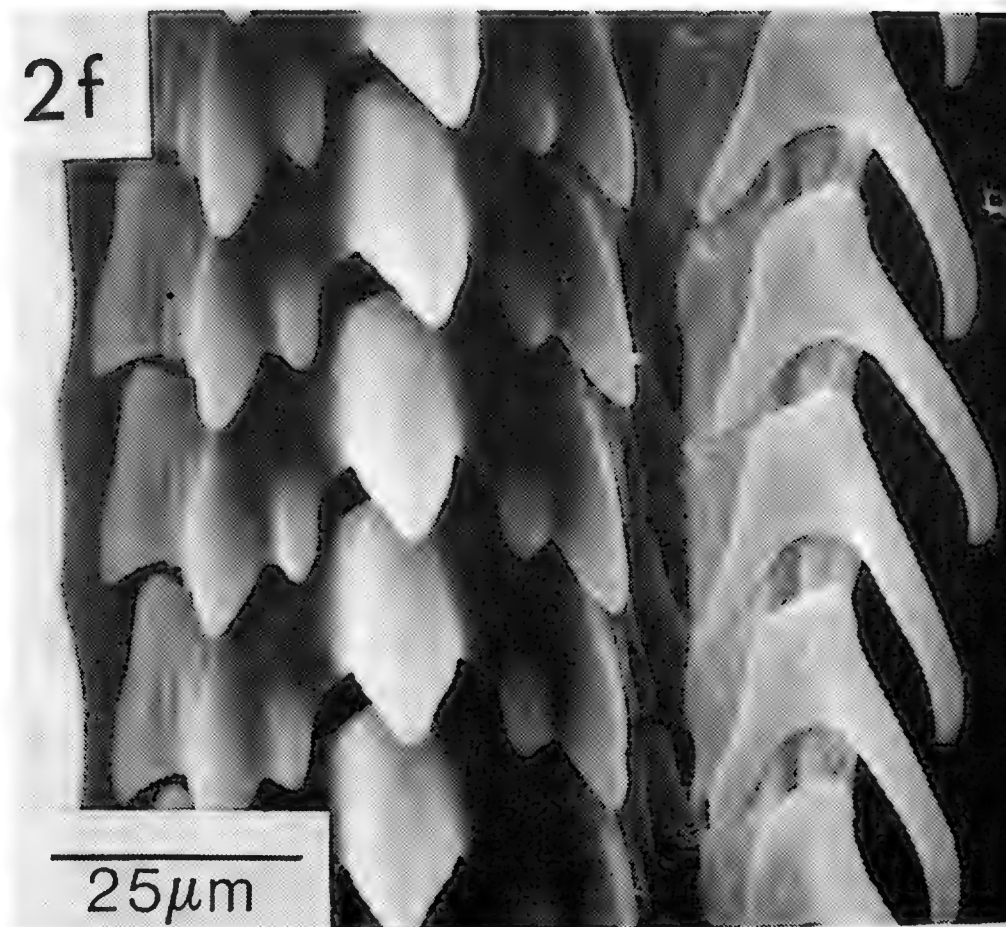
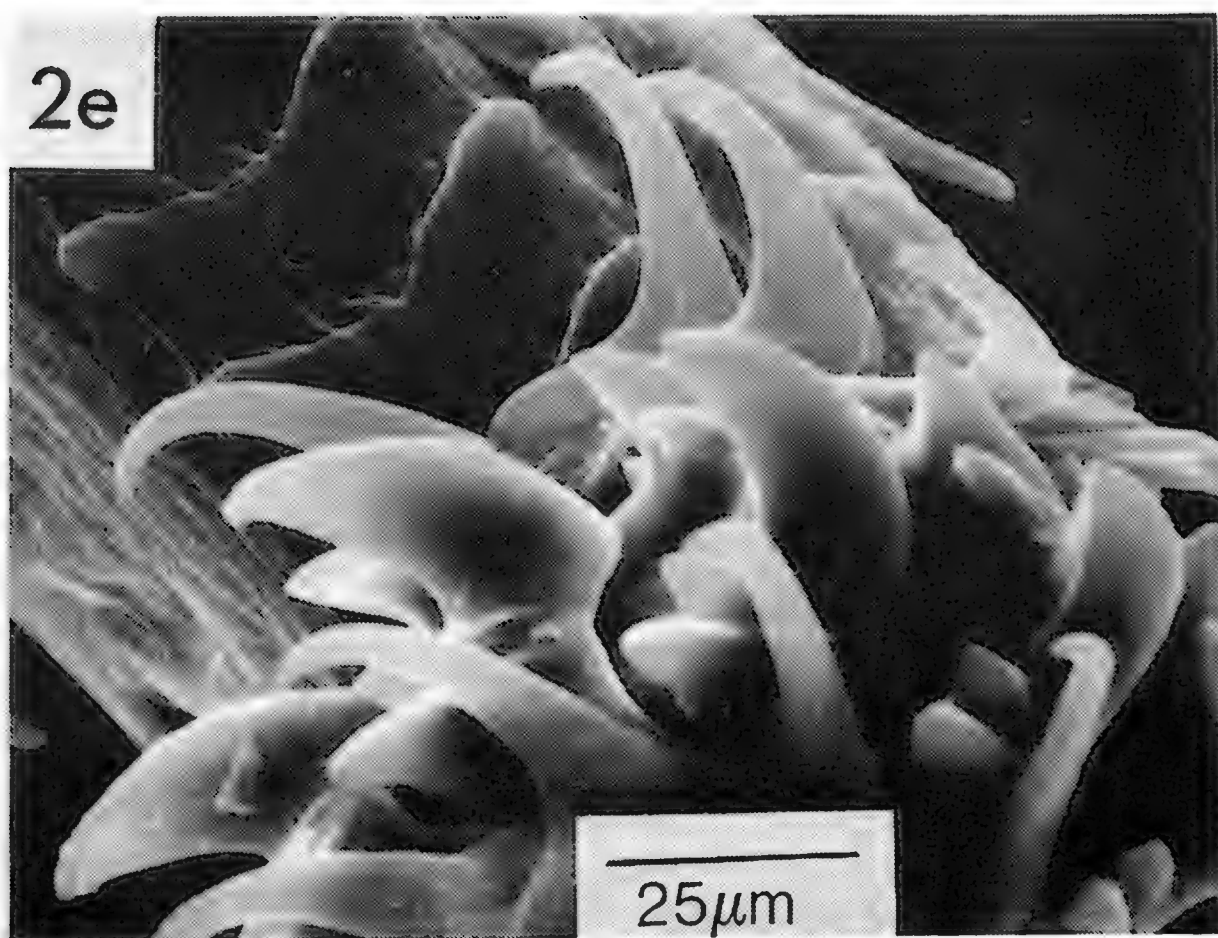
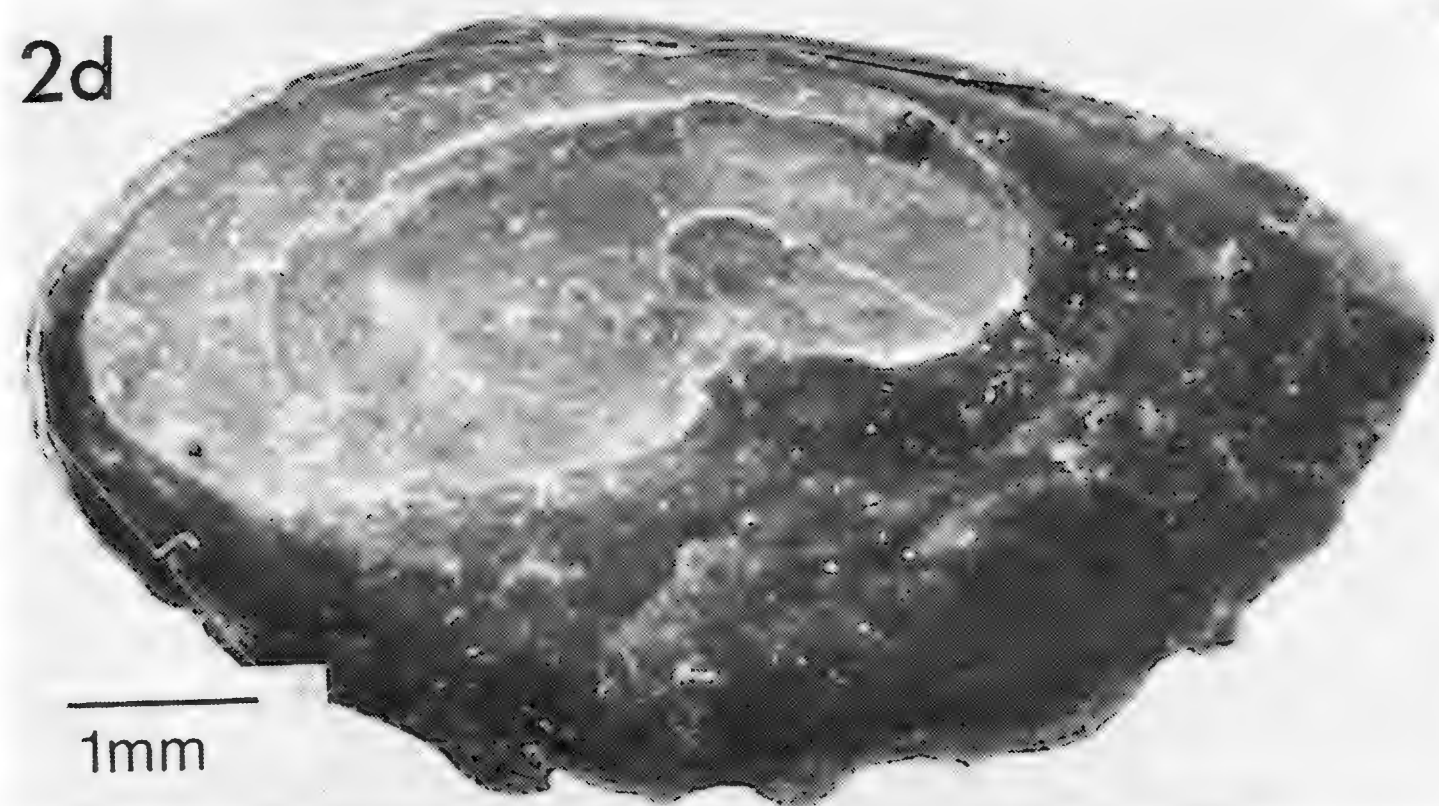
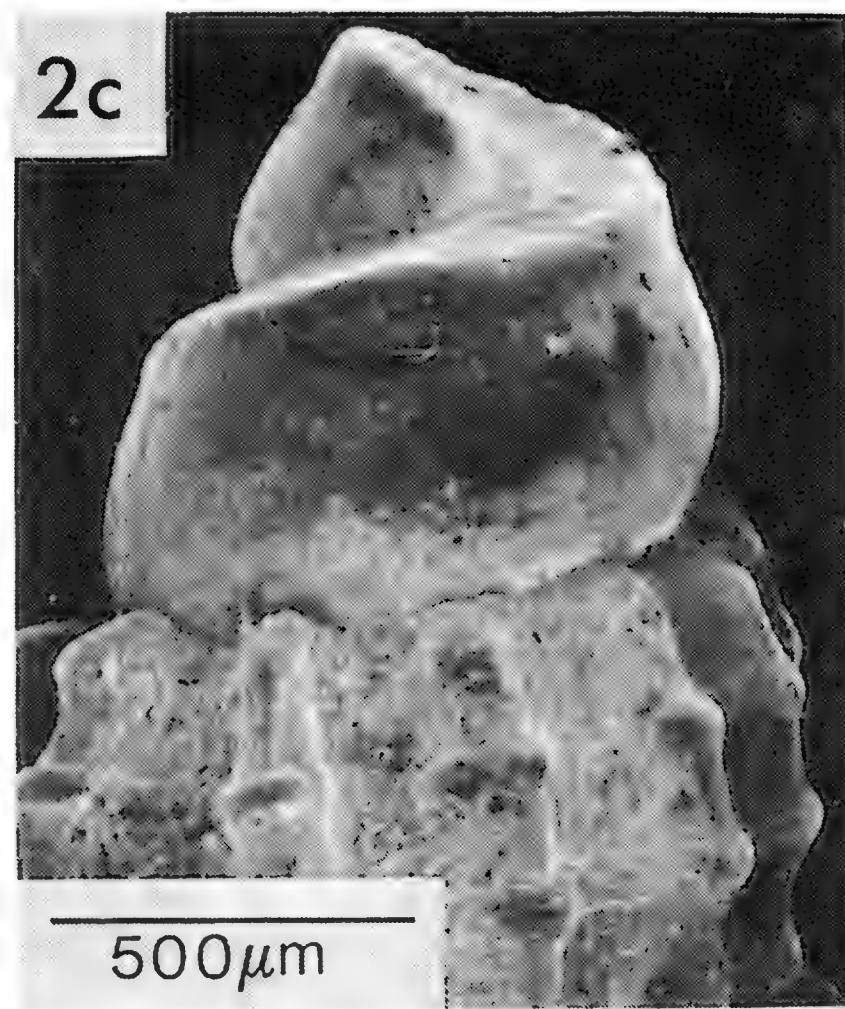
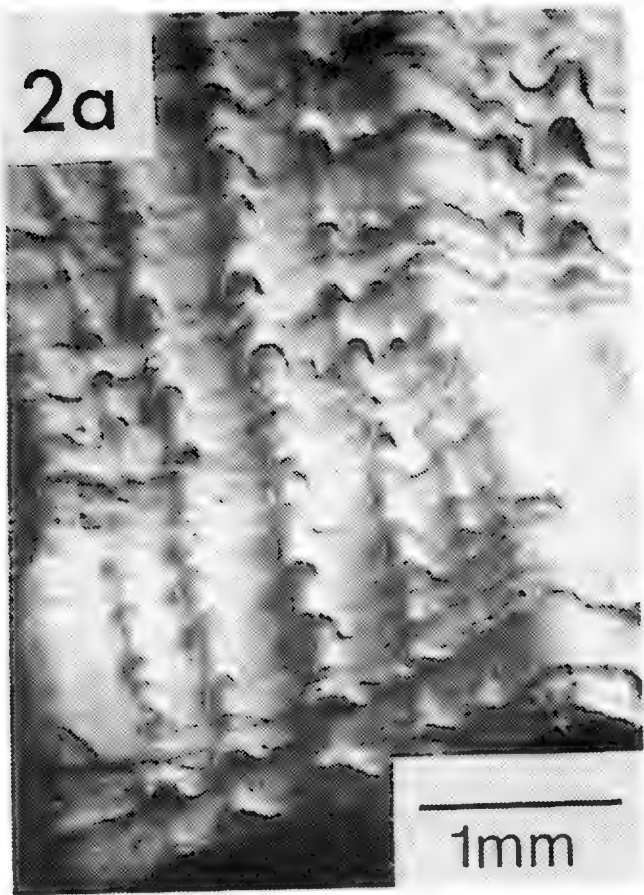
*Muricopsis omanensis* n.sp. Holotype NMW.Z.1985.043.1

1a Abapertural view, 1b Apertural view

PLATE 19 (overleaf)

Scanning Electron Micrographs of *Muricopsis omanensis* n.sp. 2a Detail of spiral sculpture, Paratype NMW.Z.1985.043.2; 2b Fine detail of spiral sculpture, Paratype NMW.Z.1985.043.2; 2c Protoconch of Holotype; 2d Operculum of Paratype NMW.Z.1985.043.2; 2e, 2f Radula of Paratype NMW.Z.1985.043.4





### Remarks

*M. omanensis* at first sight more closely resembles some of the Thaiininae because it lacks any spinose sculpture; also the radula is similar to that of many Thaiids, but this applies to several species in the Muricininae. However, after extensive comparison in literature and in collections we decided tentatively to place it in the genus *Muricopsis*. Most species of *Muricopsis* possess spinose sculpture, but if this is worn or weak in specimens of *M. blainvillei* there is an obvious similarity. The pattern of apertural denticles and columellar folds is identical between *M. omanensis* and *M. blainvillei* down to the spacing between denticle 1 and the remaining 4. From *M. blainvillei*, *M. omanensis* differs in the consistent lack of spines, the lack of shouldering on the whorls, the colour pattern and the radula. The colours of *M. blainvillei* although variable are not so rich a mahogany, overlain with purple-black but are less striking shades of dull tan, brown or grey with apertures of white to a dull rose. The central cusp of the rachidian tooth in *M. blainvillei* is smaller than the lateral cusps: the opposite condition exists in *M. omanensis*. The radula of *M. omanensis* most closely resembles that of *M. zeteki* (see figure on page 6 in Radwin and Attilio 1976). Although *Muricopsis* has a worldwide distribution in warm waters and similarity between *M. omanensis* and *M. blainvillei* may suggest a tethyan link.

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# GEOGRAPHICAL VARIATION IN *RUPESTRELLA* *DUPOTETII* (TERVER) (GASTROPODA: CHONDRINIDAE) FROM MOROCCO AND ALGERIA

D. T. HOLYOAK<sup>1</sup> AND MARY B. SEDDON<sup>1</sup>

(Accepted for publication, 19th October, 1985)

**Abstract:** The distribution, subspecific variation and genital anatomy of *Rupestrella dupotetii* are described. Populations recently discovered in NE. Morocco and NW. Algeria have smaller, narrower shells than those from further east in N. Algeria; they are named as *R. d. sebouensis* subsp. nov.

## INTRODUCTION

The genus *Rupestrella* contains rock-dwelling land snails found mainly in the Mediterranean region. They have often been treated as part of the genus *Granopupa* but Gittenberger (1973, pp. 21–22) has given reasons for their separation. The last comprehensive review (Pilsbry 1918) recognised about sixteen species, of which eight are known only in north Africa and five only in Sicily.

A shortage of specimens has prevented revision of the north African forms. The present paper considers the distribution and geographical variation of *R. dupotetii* (Terver) on the basis of published information and new collections made in July and August 1984. Specimens from NE. Algeria resemble those hitherto described as *R. dupotetii*, but little known populations from much further west in NW. Algeria and NE. Morocco have shells that are narrower and usually smaller. It is undesirable to treat the eastern and western groups of populations as distinct species because the known differences between them are only in shell width and size and these may not involve large genetic differences. However, subspecific separation of the two groups of populations is desirable because specimens from each group are clearly separable and the characters of both are consistent at several widely spaced localities. Furthermore, each of them occupies a discrete range separated by over 400 km in which neither form has been found, so it is unlikely that a clinal pattern of variation is involved. Hence, the western populations are named as *R. d. sebouensis* subsp. nov. below.

## ***Rupestrella d. dupotetii* (Terver, 1839)**

1839. *Vertigo Dupotetii* Terver, pp. 32–33, pl. 4, f. 12–13.

1839. *Pupa rupestris* (Bul.) Phil., syn. *Torquilla Dupotetii* (?) sec. Parr. in litt., *Vertigo Dupotetii* Terver: Rossmässler (not Philippi, 1836), pp. 25, 44, pl. 49, no. 637.

1841. *Pupa rupestris* Rossmässler (not Philippi, 1836) in Wagner, p. 250.

1853. *Pupa rupestris* Phil. (not Philippi, 1836), syn. *Vertigo Dupotetii* Terv.: Morelet, pp. 292, 301.

<sup>1</sup> Department of Geography, University of Nottingham, Nottingham NG7 2RD.

1864. *Vertigo Dupoteti* Terver: Bourguignat, pp. 96–97, pl. 6, f. 25–27.  
 1870. *Vertigo Dupoteti* Letourneux, [offprint pp. 9, 13, 17, 20, 30].  
 1870. ? *Pupa eucyphogyra* Letourneux, p. 311, pl. 6, f. 8–10.  
 1883. ? *Pupa dupontii* Paetel, p. 107.  
 1886. *Vertigo Dupoteti*: Kobelt, p. 58.  
 1886. *Pupa Dupotetii* Terver: Kobelt, p. 66.  
 1886. *Pupa Dupoteti*: Kobelt, p. 71.  
 1893. *Vertigo Dupoteti* Terver (*Pupa rupestris* Rossmässler): Letourneux [& Bourguignat ?] in Hanoteau & Letourneux, p. 292.  
 1898. *Torquilla rupestris* Phil. (not Philippi, 1836), *Torquilla dupoteti* Terv., ? *Torquilla eucyphogyra* Let.: Kobelt, p. 248.  
 1918. *Granopupa dupoteti* (Terver): Pilsbry, pp. 349–350, pl. 47, f. 7, 8.  
 1918. ? *Granopupa eucyphogyra* (Let.): Pilsbry, pp. 350–351, pl. 47, f. 6.  
 1939. *Granopupa Dupoteti*: Pallary (1939b), p. 108.

#### *Description of shell*

Distinct from all other N. African *Rupestrella* in lacking any apertural teeth, and from most of the other species in its smaller shell (Fig. 1). *R. rupestris* (Philippi, 1836) from Sicily has a shell of similar size and form, but according to Pilsbry (1918, p. 352) it is ‘much more strongly ribbed than the Algerian *dupoteti*, with which some authors have confused it.’ Bourguignat (1864, p. 97) noted that the striation on shells of *dupoteti* was stronger in some populations than in others.

For measurements of shells see Table 1. Our measurements agree well with those of Terver (1839, p. 32) who gave “longeur 1 ligne  $\frac{1}{2}$  à 2 lignes, diamètre 1 ligne” [i.e.  $3\text{--}4 \times 2$  mm].

#### *Genital anatomy*

Two specimens from SE. of Bejaïa were dissected (Fig. 2A). The anatomy of the distal genitalia resembled that briefly described by Gittenberger (1973, p. 21) for *R. philippii* (Cantraine, 1841), which appears to be the only species of the genus for which the genitalia have been described hitherto.

#### *Distribution*

Northern Algeria from near Lakhdaria (Gorges of the Isser) eastwards to near Annaba; Fig. 3 summarises records from the literature listed above and our own field collecting.

#### *Ecology*

Published records are all from rocky crags or gorges, mainly of limestone, but of schist in the Djurdjura (Letourneux 1870). Terver (1839) noted that it was living with *Helix rupestris* [i.e. *Pyramidula rupestris* (Draparnaud)] at one locality. Both of our own finds were on limestone sea-cliffs with patchy cover of grasses and herbs on ledges; a few bushes were present at both sites, but not enough to give much shade.

### ***R. d. sebouensis* subsp. nov.**

syn. *Pupa Dupotetiana*: Pallary (1939a), p. 65 [*nomen nudum*; apparently intended as an emendation of *dupotetii*].

#### *Description of shell*

Generally similar to shells of *R. d. dupotetii*, but always less broad with proportionately smaller aperture, and usually smaller overall (Fig. 1). See Table 1 for comparison of shell measurements.



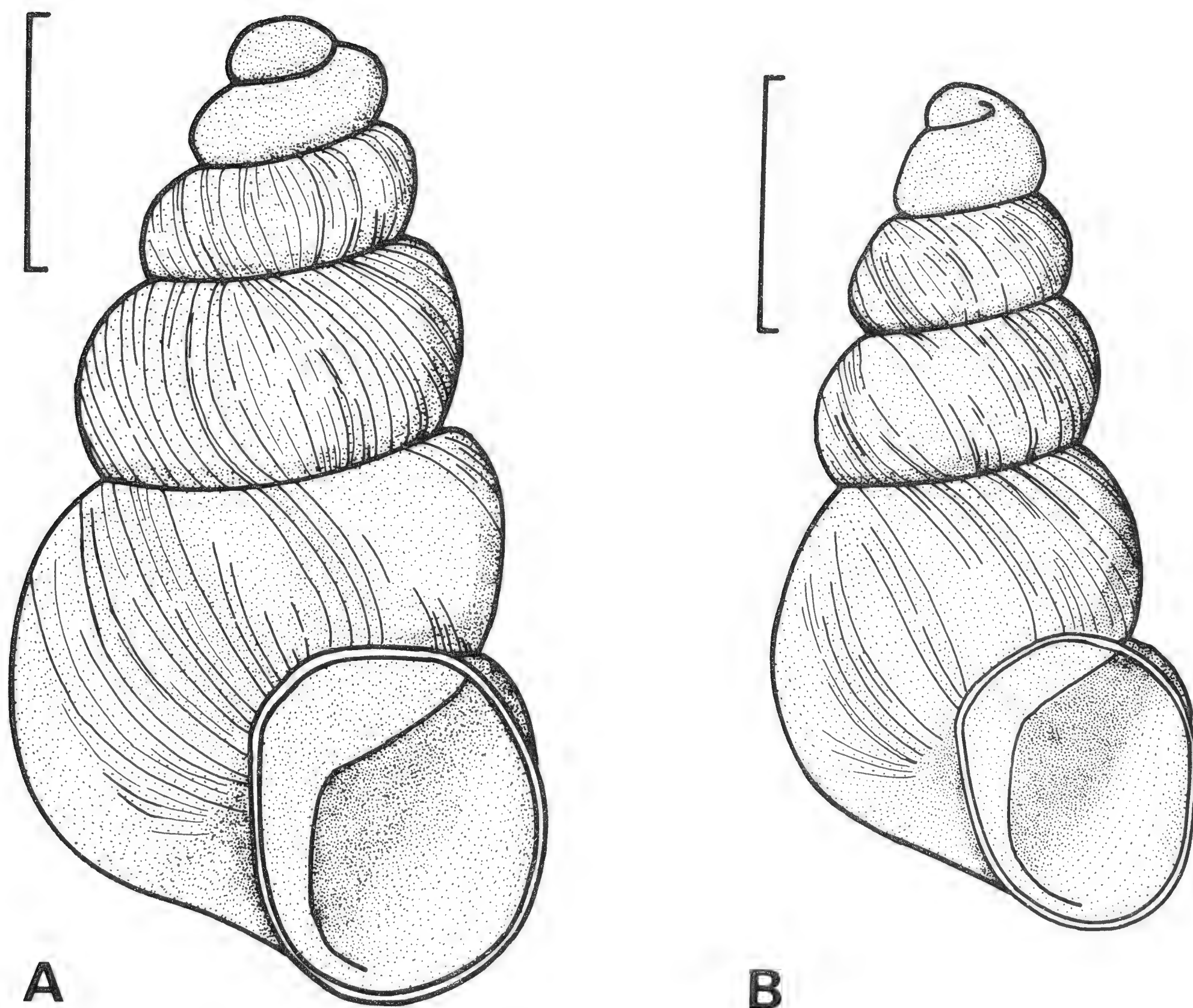


Fig. 1. Shells of *Rupestrella dupotetii*. A *R. d. dupotetii* from SE. of Bejaïa, Algeria; B *R. d. sebouensis* subsp. nov., Holotype; scale lines represent 1.0 mm.

#### *Genital anatomy*

One specimen from the type locality was dissected (Fig. 2B). The distal genitalia were generally similar to those of *R. d. dupotetii*, differing in being proportionately smaller and more slender with the penis sheath less tightly folded. These differences may be due to the specimen dissected being somewhat immature.

#### *Distribution*

Found at four localities in 1974 (see Fig. 3):

- (1) (Type locality) above gorge of Oued Sebou, c. 6 km W. of El Menzel, Moyen Atlas, Morocco (33°51'N., 4°36'W.); c. 720 m elevation;
- (2) by S5306 road c. 1.5 km NE. of Taforalt (SW. of Berkane), Morocco (34°49'N., 2°24'W.); c. 660 m elevation;
- (3) by S5306 road 5.5 km NE. of Taforalt (SSW. of Berkane), Morocco (34°50'N., 2°21'W.); c. 430 m elevation;
- (4) by W46 road c. 2 km SE. of Sidi Yahia, Mts. de Tlemcen, Algeria (34°43'N., 1°33'W.); c. 650 m elevation.

TABLE 1

Measurements of shells of *Rupestrella dupotetii*.

(measurements were made as shown by Kerney & Cameron (1979, p. 14), to accuracy of  $\pm 0.05$  mm; N = number measured; s = one standard derivation;  $\bar{x}$  = mean)

<i>R. d. dupotetii</i>	shell height (mm)			shell breadth (mm)			N
	range	$\bar{x}$	s	range	$\bar{x}$	s	
locality (A)	3.2–4.0	3.71	0.23	2.1–2.3	2.18	0.08	9
locality (B)	3.5–3.9	3.70	0.13	2.0–2.2	2.07	0.10	7
<i>R. d. sebouensis</i>							
locality (1) Holotype	3.3			1.7			1
locality (1) Paratypes	2.9–3.6	3.24	0.16	1.5–1.9	1.67	0.09	50
locality (2)	3.1–3.7	3.40	0.18	1.7–2.0	1.80	0.10	21
locality (3)	2.9–3.3	3.16	0.19	1.6–1.7	1.68	0.04	5
locality (4)	3.2–3.6	3.42	0.12	1.7–1.9	1.80	0.06	13

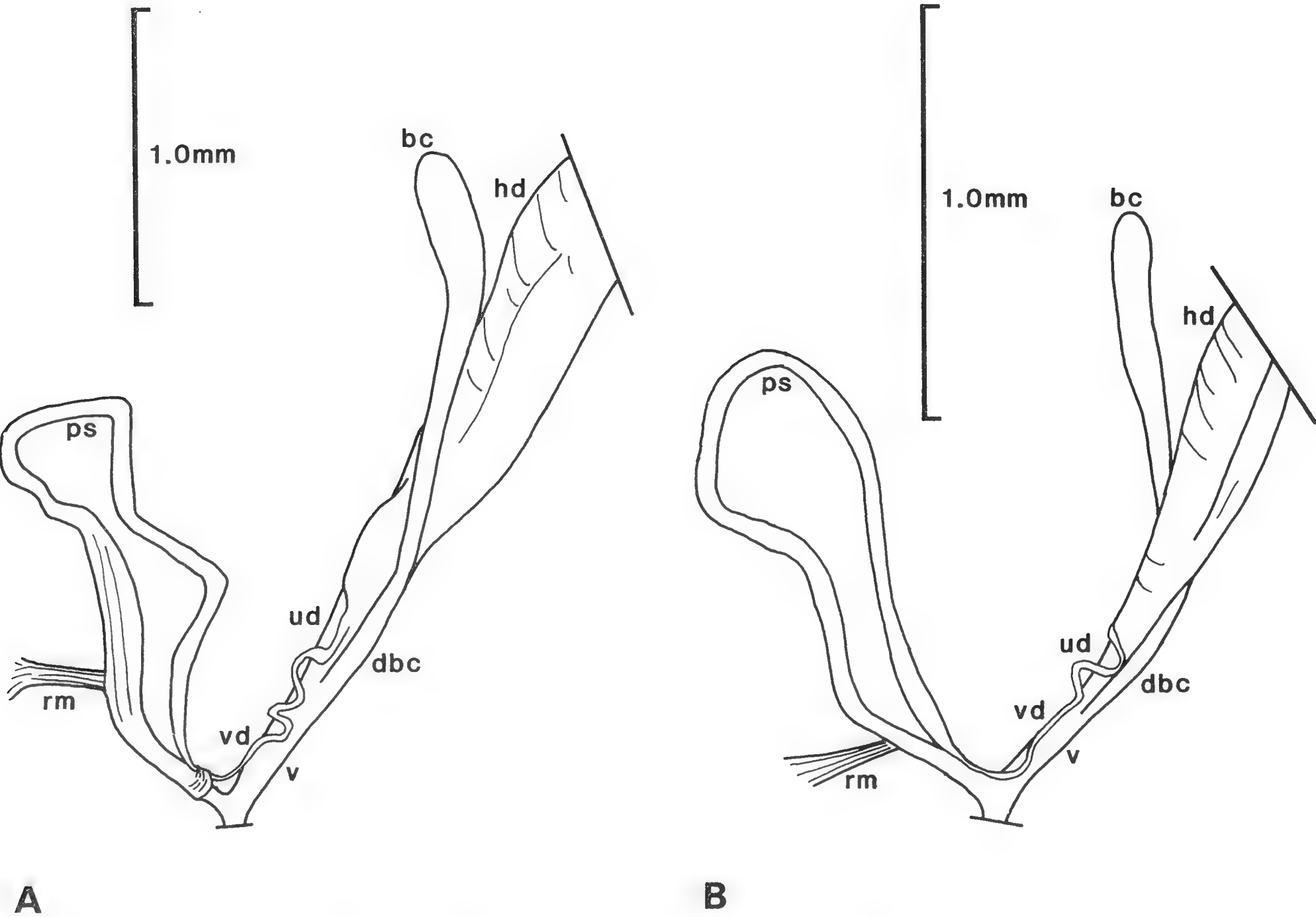


Fig. 2. Distal genitalia of *Rupestrella dupotetii*. A *R. d. dupotetii*, B *R. d. sebouensis*; scale lines represent 1.0 mm; bc bursa copulatrix (= gametolytic gland), dbc duct of the bursa copulatrix, hd second hermaphrodite duct (= ovispermiduct), ps penis sheath, rm penial retractor, ud uterine duct (= free oviduct), v vagina, vd vas deferens.

Our records are thus from three different mountain ranges: the northern part of the Moyen Atlas and Beni Snassen in NE. Morocco and the Mts. de Tlemcen in NW. Algeria. The only previous report of this species from so far to the west was by Pallary (1939a, p. 65) from the 'Massif des Traras' (see Fig. 3); Pallary commented 'c'est la seule localite occidentale ou soit localisée cette espece'. It is likely that further collecting will produce additional records in these regions.

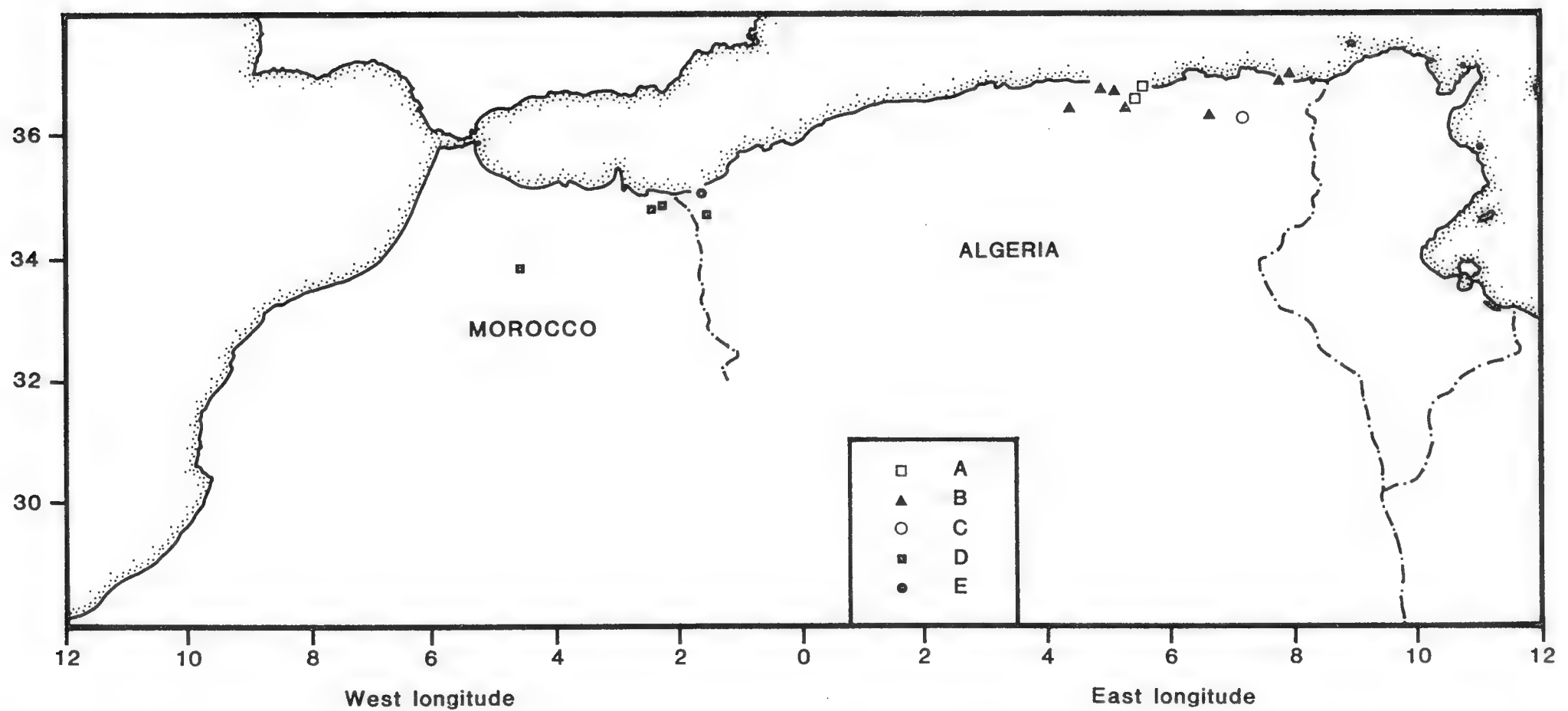


Fig. 3. Distribution of *Rupestrella dupotetii* in NW. Africa. *R. d. dupotetii*: A authors' records, B records from literature, C uncertain record (of '*eucyphogyr*'); *R. d. sebouensis*: D authors' records, E uncertain record (from Pallary 1939a).

Holotype: lodged in Department of Zoology, National Museum of Wales, registration number NMWZ 1985.103.1.

Derivatio nominis: from the Oued Sebou.

### Ecology

All four of our records are from crags of calcareous rock (limestone, calcareous sandstone) in mountain regions. Specimens were collected from ledges with patchy growth of grasses and herbs and no more than slight shading from bushes or trees. At the type locality living animals were aestivating on bare nearly vertical limestone.

### ACKNOWLEDGEMENTS

Thanks are due to M. Holyoak for assistance with fieldwork and to the Department of Zoology, National Museum of Wales for much help in consulting literature.

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## AN UNDESCRIBED *LEIOSTYLA* (GASTROPODA: PUPILLIDAE) FROM MADEIRA

D. T. HOLYOAK<sup>1</sup> AND MARY B. SEDDON<sup>1</sup>

(Accepted for publication, 14th December, 1985)

*Abstract:* An undescribed *Leiostylia* collected on Madeira in 1984 is named as *L. filicum* sp. nov. It shows characters that appear to connect *L. (Scarabella) cassida* with *Leiostylia* subgenus *Leiostylia*.

### INTRODUCTION

Among *Leiostylia* we collected in December 1984 from the Caldeirão Verde in northern Madeira were 13 specimens that we could not identify. Initial comparison with the descriptions and figures in the detailed review by Pilsbry (1922–1923) suggested these were an undescribed species and this impression has been confirmed by study of the comprehensive collections of Madeiran *Leiostylia* in the British Museum (Natural History) and National Museum of Wales, which together include type material of all similar species.

### ***Leiostylia filicum* sp. nov. (Fig. 1)**

#### *Description*

The shell is of 7–7.5 whorls and ovate-conic with shallow sutures; it is only moderately solid and rather translucent. The first five whorls form an almost conical spire occupying nearly one-third of the total shell height; the penultimate whorl and body whorl are rounded and together they occupy more than two-thirds of total shell height. The umbilicus is small and deep. The surface of the shell has strong but rather irregular ribbing that becomes weak towards the umbilicus; faint traces of spiral sculpture are also present on the last two whorls; the protoconch and second whorl are smooth. In colour the shell is bright red-brown with an ill-defined yellow-brown sub-medial band on the body whorl and conspicuous irregular whitish longitudinal streaks. The aperture is subtriangular with a concavity in the upper palatal part of the peristome. The peristome is slightly thickened and strongly reflected, especially below. Six whitish apertural teeth are present. The upper parietal tooth emerges from the mouth and forms a tall narrow ridge that disappears from view deep inside the mouth. The lower parietal tooth is also tall but less so than the upper parietal and not emergent; it disappears from view deep inside the mouth. The strong columellar tooth emerges onto the peristome and forms a tall narrow ridge that continues deep into the shell mouth. The basal tooth is a short and low brownish or whitish callus rather deep inside the mouth. The palatal tooth begins well below the peristome, rises to a sharp high ridge and then descends to form a narrow line of thickening that continues back into the shell mouth. The upper palatal tooth is very weak, consisting of a slight thickening not far beneath a prominent whitish callus on the inside of the peristome.

In the juvenile shell the periphery is sharply angled and there are two very tall and narrow white apertural teeth, one parietal and one columellar.

<sup>1</sup> Department of Geography, University of Nottingham, Nottingham NG7 2RD.

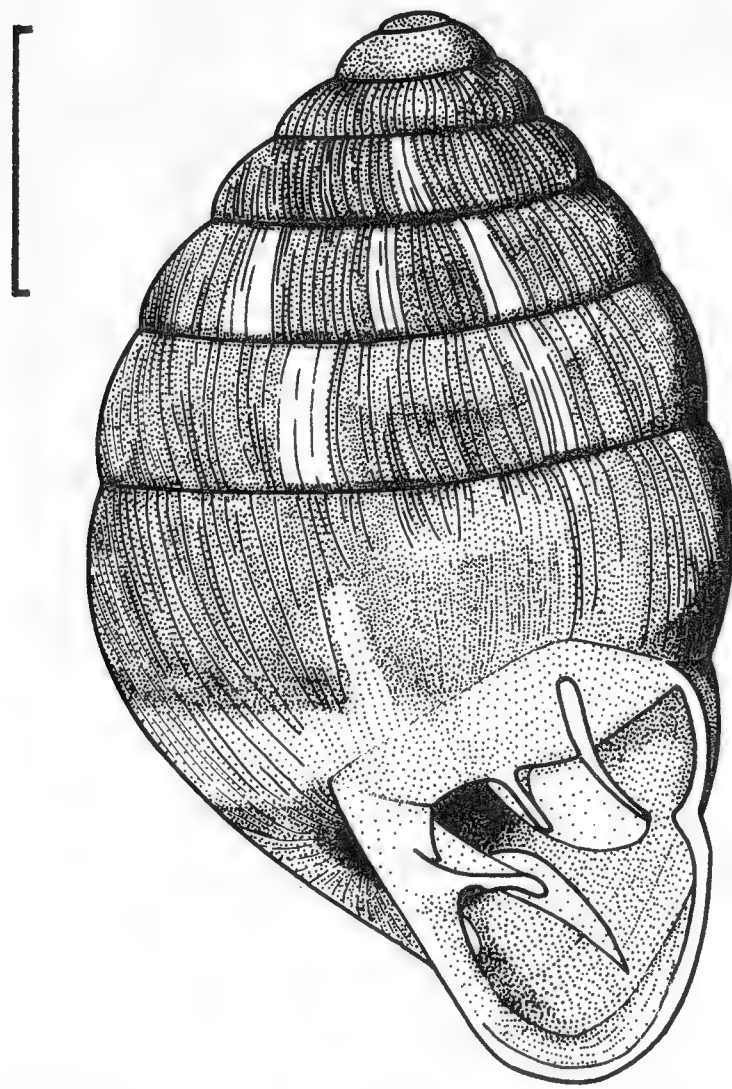


Fig. 1. Shell of Holotype of *Leiostyla filicum* sp. nov. The scale line represents 1.0 mm.

#### Measurements

Holotype height 4.0 mm, breadth 2.4 mm; paratypes 3.3–3.8 × 2.3–2.4 mm.

#### Comparisons

Resembles *L. (Scarabella) cassida* (Lowe, 1831) in the ventricose shape, shallow suture, white longitudinal streaking on a red-brown shell and rather narrowly triangular shell mouth. However, it differs sharply from *L. cassida* in its smaller size, absence of an upper columellar tooth, fewer palatal teeth, shorter lower palatal tooth that does not reach the peristome and differently shaped peristome. In these respects *L. filicum* appears to form a link between the monotypic subgenus *Scarabella* and subgenus *Leiostyla sensu stricto*.

None of the other Madeiran *Leiostyla* show much resemblance to *L. filicum*. In *L. cheilogona* (Lowe, 1831) the apertural teeth are generally similar but that species has a considerably smaller and narrower shell of a uniform light brown colour, with much weaker ribbing. Shells of *L. cassidula* (Lowe, 1852) are also considerably smaller and narrower; that species also differs in having an upper columellar tooth and in having the supraparietal tooth joined by a callus to the angular tooth.

#### Type Locality

In the Caldeirão Verde, 6.5 km SW. of Santana in northern Madeira at c. 1000 m elevation. Material: Besides the Holotype (lodged in the National Museum of Wales, Cardiff as NMWZ 1985.108), 12 paratypes from the same locality (one of them lodged in British Museum (Natural History), others in the authors' collection).

#### Ecology

The living snails were collected from stems and fronds of ferns saturated by spray from a large waterfall. Specimens were obtained by shaking these ferns over a sieve. Other snails collected from the same place using this technique were: *Craspedopoma mucronatum* (Menke) (52), *Columella microspora* (Lowe) (5), *Leiostyla cheilogona* (Lowe) (9) and *Leptaxis membranacea* (Lowe) (10).



*Derivatio nominis*  
Of the ferns (*filicum*).

#### ACNOWLEDGEMENTS

Thanks are due to the staff of the Mollusca sections at the British Museum (Natural History) and National Museum of Wales for helpful access to specimens and literature in their care.

#### REFERENCE

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## REVIEW

*Monograph of the Genus Cancellaria* by G. B. Sowerby. Originally published in the *Thesaurus Conchylorum*, vol. 2, pp. 439–461, pls. 92–96 (in colour), London, 1849. Facsimile edition with an *Update* by A. Verhacken, 11 pp., Luis Pisani Burnay Publisher, Lisboa, 1985. Price \$8.

This is one of the earliest pictorial Monographs devoted to the genus *Cancellaria*. It describes 68 Recent species, 41 of which were introduced to science by members of the Sowerby family prior to the publication of this Monograph. Though there are no new species descriptions in it, the Monograph is a valuable source material for the 41 'Sowerby species' and it can be helpful in settling controversial identification problems, until a modern revision of the genus/family becomes available.

The descriptions are in Latin with short comments and locality data in English. The text is accompanied by 106 colour drawings of natural size. The original illustrations were of excellent quality, never surpassed in the rest of the 19th century, and they are reproduced well in the facsimile edition. The 6 colour plates are printed on strong, stiff paper and are kept in a pocket attached to the back cover of the booklet. Several species were illustrated here for the first time and 15 of them have later been designated as type species of some of the new genera and subgenera into which the Lamarckian genus *Cancellaria* has subsequently been split.

The number of species described is less than a third of the Recent *Cancellaria* species known today, and some of the names used here are now considered to be junior synonyms. Nevertheless, the Monograph contains a high proportion of the Recent *Cancellaria* species found in museums and private collections, shells which conchologists are likely to come across. A particularly useful feature of this facsimile edition is the *Update* by the Belgian conchologist Verhacken, a long-time student of the genus *Cancellaria*. This gives the current taxonomic position of all the 68 species including synonymy, homonymy, spelling mistakes, generic placement and correct locality data where applicable. It is very concise, but clear-cut and well arranged.

All in all, this well-produced and reasonably priced little book is a useful addition to the library of every conchologist who is interested in the genus *Cancellaria*. It contains many fine illustrations and some valuable source material which is otherwise inaccessible to many conchologists.

E. SÁNDOR

# AN UNDESCRIBED SPECIES OF *SPHAERIUM* (BIVALVIA: SPHAERIIDAE) FROM THE NORWICH CRAG (EARLY PLEISTOCENE) OF EAST ANGLIA

D. T. HOLYOAK<sup>1</sup> AND R. C. PREECE<sup>2</sup>

(Accepted for publication, 14th December, 1985)

**Abstract:** An undescribed freshwater bivalve from Early Pleistocene marine deposits in East Anglia is named as *Sphaerium icenicum*. Eight valves from four sites in the Norwich Crag are assigned to this form.

Whilst preparing a review of the Quaternary non-marine Mollusca of the British Isles we encountered specimens of an unidentified species of the freshwater bivalve genus *Sphaerium* in museum and private collections. These had been collected from the sandy marine deposits of the Early Pleistocene Norwich Crag Formation of East Anglia, in which shells of land and freshwater Mollusca occur consistently but at very low frequency, amongst a predominance of marine shells. Dr. M. P. Kerney, in an unpublished review of British Pleistocene Mollusca (1959), had recognised that this represents an undescribed form and given it a manuscript name on the basis of the five valves then available. Three more valves have since been recognised among material collected in 1979 by P. G. Cambridge and Dr. P. E. Long and these were accompanied by a valve of *S. corneum* (Linnaeus). This is the first record of a typical specimen of *S. corneum* from the Norwich Crag and it is important because the form described here had hitherto been confused with *S. corneum*.

## ***Sphaerium icenicum* sp. nov.** (Fig. 1, Plate 20)

1879. *Cyclas cornea*: Reeve, p. 71 [not *cornea* Linnaeus, 1758].  
1881. *Sphaerium corneum*: Woodward, p. 43 [not *corneum* Linnaeus, 1758].  
1899. *Sphaerium corneum* (Linné): Kennard & Woodward, p. 202 [part, not *corneum* Linnaeus, 1758].  
1914. *Sphaerium corneum*: Harmer, vol. 1, p. 42 [part, not *corneum* Linnaeus, 1758].  
1959. *Sphaerium* (?*Cyrenastrum*) *icenicum*, sp. novum, Kerney MS., pp. 349–351, pl. 11, figs. 4a, b.

**Description of Holotype** (right valve): Shell compressed, somewhat quadrate in outline, truncate posteriorly. Umbones nearly central, directed anteriorly. Shell solid, thicker than usual in *S. corneum*; surface with strong regular, close-set and sharply-cut concentric striae, becoming more pronounced marginally. Hinge-plate arcuate, rather strong. Ligament-pit distinct (posterior part missing due to breakage). c3 prominent, sharply arched, pi and piii long, straight, slightly diverging posteriorly; ai and aiii much shorter; ai projecting ventrally from hinge-plate. Cardinal teeth closer to the apices of the anterior laterals than to those of the posterior laterals. Adductor impressions and pallial line not visible.

**Measurements of Holotype:** Length 10.2 (slightly damaged), height 7.9 mm.

**Holotype of Type Locality:** From Norwich Crag at Sizewell, Suffolk (NGR TM 475639),

<sup>1</sup> Department of Geography, University of Nottingham, University Park, Nottingham NG7 2RD.

<sup>2</sup> Sub-department of Quaternary Research, The Godwin Laboratory, Free School Lane, Cambridge CB2 3RS.





Fig. 1. Holotype of *Sphaerium icenicum* sp. nov. from the Norwich Crag at Sizewell, Suffolk; drawn by Dr. M. P. Kerney; the scale is marked at intervals of 1.0 mm.

collected by Dr. P. E. Long in 1958; lodged in Department of Palaeontology, British Museum (Natural History), registration no. LL28141.

*Paratypes*: (1) Left valve ( $9.7 \times 7.2$  mm); Norwich Crag at Thorpe, Norfolk [approximate NGR TM 4398], collected by F. W. Harmer; in Collection of Department of Palaeontology, British Museum (Natural History), registration no. L33927 (presented by Sir. S. F. Harmer in 1923).

(2) Left valve ( $9.4 \times 7.2$  mm) from Norwich Crag at Thorpe, Norfolk; in J. B. Wigham Collection at Norwich Castle Museum; accession no. 338.985 (1a) [Fossil catalogue no. 860].

(3) Left valve ( $9.0$  (broken)  $\times 7.0$  mm); same locality and Collection as paratype (2), accession number 338.985 (1b) [Fossil catalogue no. 860].

(4) Fragment of valve (length at least 9.9 mm); Lower Bed, Bramerton Common (NGR TG 29510601); in J. Reeve Collection at Norwich Castle Museum, accession no. 339.985 (1) [Fossil catalogue no. 670].

(5) Somewhat worn right valve ( $9.3 \times 7.1$  mm); Norwich Crag at Bulcamp Union Pit (NGR TM 442757), Suffolk, collected by Dr. P. E. Long in 1979; in Collection of Dr. Long. From the recent excavations at this site of which details are given by Cambridge (1982) and Funnell (1983).

(6) Worn right valve ( $7.5 \times 5.7$  mm); same locality details as (5), but collected by P. G. Cambridge.

(7) Broken and very worn left valve (height at least 6.8 mm); same locality and collector as (6).

*Description of left valve* (paratype no. 1):

Similar to right valve in shape, thickness, sculpture and in the form and orientation of the umbones. Ligament pit narrow, not clearly visible. c4 thin, straight, oblique (crest worn away); eroded remnant of c2 solid and triangular. aii and pii both straight and projecting prominently from hinge-plate ventrally. pii distinctly longer than aii with its apex nearly twice as far from that of c2.

*Derivatio nominis*: From the Icenian, a stage name formerly applied to the Norwich Crag, Weybourne Crag and Chillesford horizon (Harmer 1920).

### Comparisons

Juveniles of *S. rivicola* (Lamarck) of a comparable size are clearly different in having a weaker hinge and less prominent umbones. *S. dickinii* (Clessin) has the lower margin of the shell nearly straight (sometimes slightly concave), not gently rounded and convex as in *S. icenicum*. It differs from *S. solidum* (Normand) in being much less tumid, more closely and more weakly striated and having an elongate, slightly quadrate form, not a rounded-triangular outline. Typical forms of *S. corneum* have a thinner, less strongly striate shell. Unusually thickened forms of *S. corneum* (such as those described as *S. bulleni* Kennard, 1911 and *S. radleyense* Kennard & Woodward, 1924 (cf. Ellis 1978)) have a more tumid shell and more rounded and less quadrate outline. The record of a typical shell of *S. corneum* from the Norwich Crag at Bulcamp provides further evidence for the distinctness of *S. icenicum*.

### Geological notes

Recent studies of the Norwich Crag Formation have disclosed that an interglacial stage ('Bramertonian') and a later cold stage ('Pre-Pastonian a') are represented at Bramerton (Funnell, Norton & West 1979). West & Norton (1974) had earlier shown that a pollen assemblage similar to that of the Bramertonian occurs in the Norwich Crag of Sizewell and other Suffolk sites. It is not however, possible to securely relate most of the specimens of *Sphaerium* described in this paper to these stages.

### ACKNOWLEDGEMENTS

Thanks are due to P. G. Cambridge and Dr. P. E. Long for access to several of the specimens and to the Department of Palaeontology, BM(NH) and Norwich Castle Museum for assistance. Special thanks are due to Dr. M. P. Kerney for generously providing much of the information on which this paper is based and for allowing us to use his unpublished drawings.

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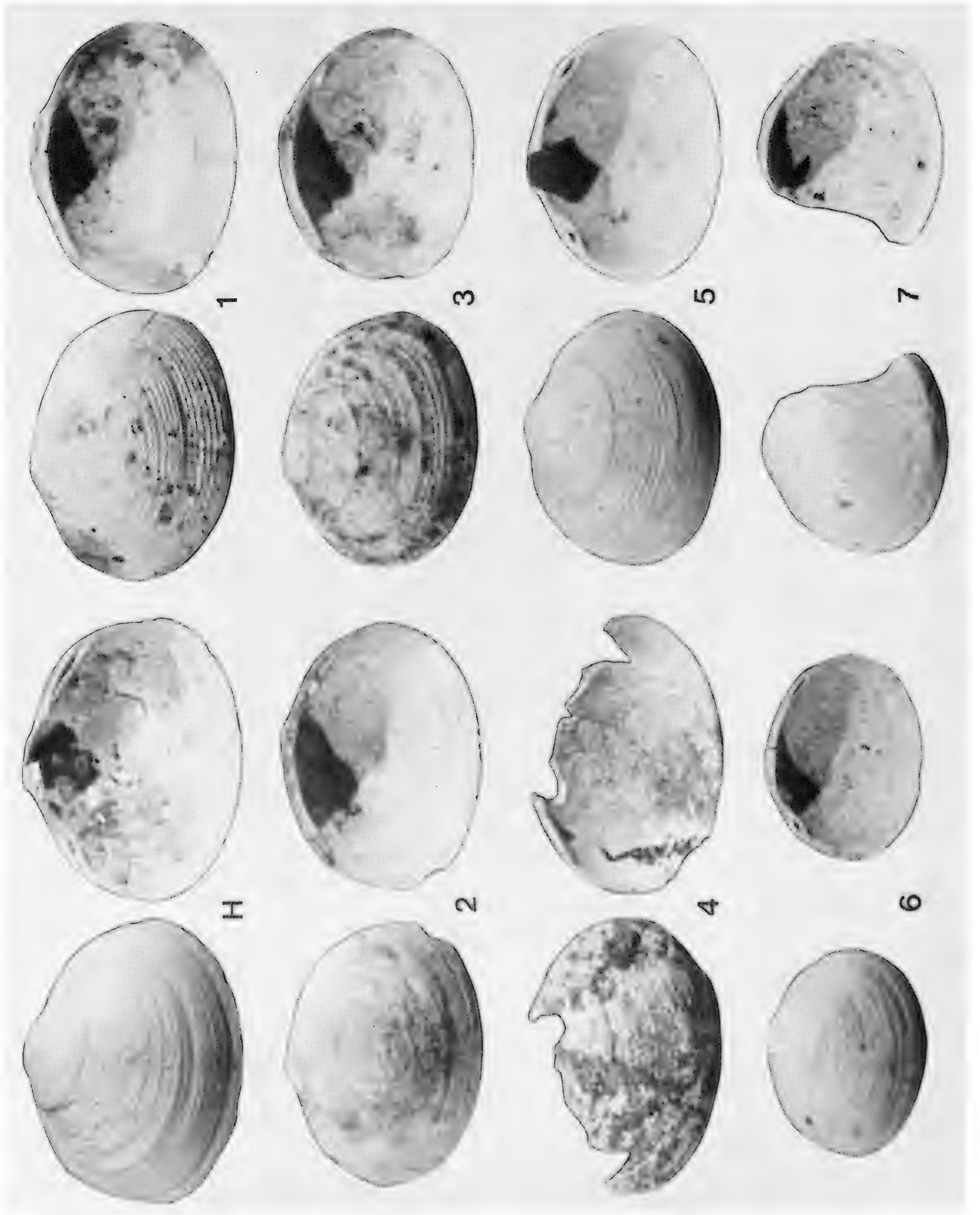


PLATE 20

*Sphaerium icenicum* sp. nov. from the Norwich Crag. H Holotype; 1-7 Paratypes numbered 1-7 (see text).



## COMMUNICATIONS

### A REASSESSMENT OF SOME BRITISH PLEISTOCENE LAND SNAILS

Whilst reviewing British Quaternary non-marine Mollusca several records of uncommon interglacial land snails have been reassessed.

*Truncatellina callicratis* (Scacchi). Most of the old published records of fossil '*Truncatellina cylindrica* subspecies *britannica* Pilsbry' other than the Flandrian records from the south coast of England have been found to represent typical *T. cylindrica* (Férussac) rather than *T. callicratis britannica*. However, Kerney (*J. geol. Soc. Lond.* **127** (1971), p. 84) reported that shells of probably Hoxnian age from the Lower Loam at Barnfield Pit, Swanscombe, Kent have apertural denticles.

Recent reexamination of *Truncatellina* from the Lower Loam collected by A. G. Davis in 1952 (housed in Department of Palaeontology, British Museum (Natural History)) has shown that both *T. callicratis* (at least two shells) and *T. cylindrica* (at least one shell) are present. In addition, recent collections from the Lower Loam have yielded two *T. callicratis* (R.C.P.) and another *T. cylindrica* (D.T.H.). These Swanscombe shells appear to be the only valid records of *T. callicratis* in Britain from before the Flandrian.

Waldén (*J. Conch., Lond.* **29** (1976), pp. 21–25) maintained *britannica* as a valid subspecies of *T. callicratis* because in this form alone the palatal denticle is the first to be reduced (although similar specimens can sometimes be found on the Continent). It is noteworthy that of the shells from the Lower Loam, the only mature specimen with the palatal part of the shell unbroken and unobscured has no palatal denticle although it has well developed columellar and parietal denticles. Another specimen with well developed columellar and parietal denticles has sediment partly obscuring the palatal side of the aperture but this shell also apparently lacks any strong palatal denticle. These specimens thus show the characters of *T. c. britannica*, raising the interesting possibility that this form (which is known only from southern England) might have existed since the Middle Pleistocene. However, additional material needs to be collected from the Lower Loam to investigate this possibility. Further investigation is also needed to examine the consistency with which the diagnostic characters of *britannica* are shown in British shells and lacking in those from continental Europe.

*Vitrinobrachium breve* (Férussac). Shells collected in recent years by D. T. H., R. C. P. and Mr. I. J. Killeen from the type Cromerian of the Upper Freshwater Bed, at West Runton, Norfolk, prompt reassessment of Vitrinidae from this and the other British Middle Pleistocene deposits. The largest shells (up to 3.4 mm in diameter) closely resemble shells of *Vitrinobrachium breve*. In the past they have been identified as *Semilimax semilimax* (Férussac) (e.g. Sparks, *Phil. Trans. R. Soc. Lond. B* **246** (1963), pp. 197–202; Sparks in West (1980) *The pre-glacial Pleistocene of the Norfolk and Suffolk Coasts*, Cambridge). However, they have the lower edge of the peristome much less cut away and exposing much less of the columellar axis than in *S. semilimax*. Somewhat less of the columellar axis is exposed than in *S. pyrenaicus* (Férussac) or *S. carinthiacus* (Westerlund). Another point of resemblance to *V. breve* rather than to *Semilimax* spp. is that the peristome descends further and more steeply below the columellar axis due to the more rounded base of the shell.

Smaller fossil shell apices from the probably Cromerian deposits at Little Oakley, Essex (one shell, Kennard Collection, B.M. N.H.) and from the probably Hoxnian tufa at Hitchin, Herts, (Kennard Collection; D.T.H. Collection) also show the characters of *V. breve* rather than the *Semilimax* spp. with which they previously have been tentatively identified (Kerney, *Proc. Geol. Ass.* **70** (1959), pp. 322–337). Hence it is doubtful if *Semilimax* spp. occur as fossils in the British Pleistocene.

*Retinella (Lyrodiscus) skertchlyi* Kerney. This species has hitherto been reported from two British Middle Pleistocene localities – the type locality at Icklingham (*J. Conch., Lond.* **29** (1976), p. 47) and Sun Hole, Cheddar (Ellis, *J. Conch., Lond.* **31** (1983), p. 191). A single juvenile shell found by R.C.P. amongst material from the interglacial tufa at Hitchin, Hertfordshire, represents the third British locality. This record strengthens the evidence that the Hitchin and Icklingham tufas are of similar age (probably Hoxnian; cf. Holyoak, Ivanovich & Preece, *J. Conch., Lond.* **31** (1983), p. 260). We provisionally retain the name *skertchlyi* (cf. Kerney, *Conchologists' Newsletter* No. 72 (1980), p. 217) until an adequate comparison can be made with similar Early Pleistocene *Lyrodiscus* from continental Europe.

*Ruthenica filograna* (Rossmässler). Two shell apices have been found in material labelled as being from 'Barrington' (Cambridgeshire). The specimens are part of the A. S. Kennard Collection housed in the Department of Palaeontology, B.M.N.H. These and a third shell apex were originally identified as *Clausilia parvula*, but the third shell is too small for species identification.

Kennard & Woodward (*Proc. Geol. Ass.* **33** (1922), p. 121) did not list either of these species for Barrington and they expressed doubts about the age of the deposits. Sparks (*Geol. Mag.* **89** (1952), pp. 163–174) showed that deposits of several different ages occur at Barrington, but the well known Barrington Beds with fossil *Hippopotamus* were shown to be Ipswichian by Gibbard & Stuart (*Geol. Mag.* **112** (1975), pp. 493–501).



The shells of *R. filograna* are almost certainly of Ipswichian age as this species is unlikely to have occurred in England except in an interglacial and a Flandrian age can reasonably be discounted. In Britain it was hitherto known only from two sites of probable Hoxnian age (Kerney, *Proc. Geol. Ass.* **70** (1959), pp. 322–337; Kerney, *J. Conch., Lond.* **29** (1976), pp. 47–50; Holyoak, Ivanovich & Preece *J. Conch., Lond.* **31** (1983), pp. 260–261).

Thanks are due to I. J. Killeen for the loan of specimens and to the Department of Palaeontology (B.M. N.H.) for helpful access to specimens in their care.

D. T. HOLYOAK\* AND R. C. PREECE

\*Department of Geography, University of Nottingham,  
Nottingham NG7 2RD  
(Received, 19th September 1985)

## LATE PLEISTOCENE LAND MOLLUSCA FROM PORTELET, JERSEY

A review by the writer of the occurrence of Late Pleistocene land Mollusca in the Channel Islands (*J. Conch., Lond.* **31** (1982), p. 57) notes that of four sites in Jersey recorded by Mourant (*A. Bull. Soc. jersiaise* **12** (1935), p. 489) two, Portelet and St. Aubin, could not be found in the late 1970s. Fieldwork in company with J. L. Monnier and J. P. Lautridou in May 1985 rediscovered the mollusc-bearing horizon at Portelet.

The shells occur in loess filling a small hollow or valley trending southwards at right angles to the coast. The loess is up to 10 m thick and the mollusc-bearing bed is in the axis of the depression about 120 m west of the steps allowing access to the bay (WV599472). The base of the main (upper) loess is strongly calcareous. This unit rests on a reddened, decalcified lower loess probably affected by interglacial weathering. The shells were recovered from a layer with calcareous concretions (Lössmanchen) up to 2 cm in long axis, and which was continuous for 10 m laterally, 2 m above the base of the calcareous loess. A bulk sample of 7.5 kg (wet weight) was passed through a no. 30 mesh (0.5 mm) sieve. This retained only shells and 23.03 g of Lössmanchen which also yielded shell fragments. By contrast with the samples from other Jersey sites, the Portelet sample was rich in shells. The following were obtained: *Succinea oblonga* Draparnaud (322 examples), *Columella columella* (Martens) (2), *Pupilla muscorum* (L.) (451), *Arion* sp. (granules, uncounted), *Deroceras* sp. (2), *Trichia hispida* (L.) (46).

Although the identity of Pleistocene succineids is often doubtful, the number of shells and their good state of preservation make it reasonably certain that the Portelet succineids are *S. oblonga*. The earlier specimens from Portelet (Mourant, *A. Bull. Soc. jersiaise* **12**, p. 489) were identified by A. S. Kennard as '*Succinea arenaria*' (= *Catinella arenaria*). These earlier specimens (Société Jersiaise Museum 1388) consist of only two shells embedded in Lössmanchen; they are poorly preserved and indeterminate.

The shells of *Pupilla muscorum* are, like those from other Jersey loess sites and from Late Devensian sites in southern England (Kerney et al., *Phil. Trans. R. Soc. Lond.* **B248** (1963), p. 160, fig. 22), taller and more cylindrical than most British Postglacial or living specimens.

The record of *Columella columella* is the first for Jersey, though the species has already been recorded in Guernsey (*J. Conch., Lond.* **31**, p. 58). Two apices and two apertures only were recovered.

In 1982 the writer proposed a broad Devensian age for the faunas examined. This still seems likely. The Portelet site with the fauna contained in loess near the base of a thick section and a little above a paleosol of interglacial character suggests that the molluscs may be Early or Middle Devensian in age rather than Late Devensian.

D. H. KEEN

Coventry (Lanchester) Polytechnic,  
Coventry CV1 5FB  
(Received, 19th October 1985)

## TOLTECIA PUSILLA (LOWE, 1831) LIVING IN BRITAIN

*Toltecia pusilla* (synonym *Punctum pusillum*) has been found living in several open-air sites in Bedfordshire, England. This is the first record of its occurrence anywhere in the British Isles.

This species is a little larger than *Punctum pygmaeum*, higher spired, with a deeper suture and a wide umbilicus. It often has low radial ribs. These may be difficult to see or be worn away. The microsculpture consists of incised spiral striations most easily seen on the underside of the shell. The shell is brown and the animal itself is very dark. The species is described and figured in Kerney et al., *Die Landschnecken Nord- und Mitteleuropas* (reviewed in *J. Conch., Lond.* **31** (1984) p. 337).

## COMMUNICATIONS

On the 15th September 1985 Mrs E. B. Rands and I visited the Stockwood Park Nurseries in Luton, Bedfordshire. The purpose of the visit was to gain distribution records for the Bedfordshire mollusc survey. The first habitat to be searched was an area of flint gravel beside a path where potted plants were placed. This unusual, strongly synanthropic habitat consists of gravel 5 to 6 cm deep underlain by a layer of black polythene sheeting. The reason for the plastic layer seems to be water retention and weed suppression. These gravel pot plant borders are watered regularly. *T. pusilla* was found almost immediately. A full list of the species found is as follows:

*Carychium tridentatum*, *Cochlicopa lubrica*, *Vertigo pygmaea*, *Vallonia costata*, *V. pulchella*, *Punctum pygmaeum*, *Toltecia pusilla*, *Arion hortensis*, *A. distinctus*, *A. intermedius*, *Vitrina pellucida*, *Vitrea sp.*, *Oxychilus draparnaudi*, *Deroceras laeve*, *D. caruanae*, *D. reticulatum*, *Boettgerilla pallens*, *Lymnaea truncatula*.

Altogether about sixty *Toltecia* were found in approximately an hour. Most of them were alive. Live animals are being kept in plastic boxes with some of the gravel from the site. They are breeding well.

Since the first discovery three other localities have been found at garden centres, all in similar habitats. The map references of the four sites are TL 085196 (Stockwood Park Nurseries), TL 096209, TL 118497 and TL 165497. *Toltecia* has been found at about one third of the garden centres and nurseries so far visited and may therefore possibly be quite widespread in southern England. The habitat requirements appear to be narrow, for even crushed granite gravel does not seem to provide a suitable substrate. *Toltecia* is apparently not frost sensitive as it occurs in unsheltered places and recent winters have included very cold spells.

*Toltecia pusilla* is widely distributed in the western Mediterranean region. It's nearest known occurrences are in Mediterranean France and in the French Pyrenees.

In Britain it is unknown as a fossil and is presumably an introduction. Although not known from greenhouses and hothouses, it is, so far, restricted to horticultural establishments. Unlike many other introduced species, it does not seem yet to have penetrated into natural or semi-natural habitats. If it proves to be firmly established in nurseries and garden centres than it will be unlike true adventives, which occur locally only for a short period before dying out.

I am grateful to Dr. M. P. Kerney for his confirmation of the species and encouragement.

D. W. GUNTRIP,  
122 Moulton Rise, Luton, Bedfordshire, LU2 0BJ  
(Received, 19th October 1985)

## A SECOND SITE FOR *LAURIA SEMPRONII* LIVING IN BRITAIN

*Lauria sempronii* (Charpentier, 1837) was collected by A. G. Stubbs in 1894 on Haresfield Beacon, Gloucestershire (SO 8209) (*J. Conch.*, Lond. **27** (1972) p. 517). The exact spot has not been located. *L. sempronii* is also known as a fossil in a few deposits of Neolithic and later age in Kent, Surrey, and Sussex (*J. Conch.*, Lond. **24** (1957) p. 183, **31** (1983) p. 158).

A second Gloucestershire locality for *L. sempronii* was found on 31 May 1985 in SO 90, east of Haresfield in a valley at 190m o.d. The habitat is 60 metres of old, somewhat tumbledown, well vegetated, limestone dry wall bordering a field and lane, sunken at one end. The species also occurs on an adjoining drystone cottage garden wall. Much of the field wall is covered by ivy (*Hedera helix* L.) of varying density, and moss, with *Geranium robertianum* L., *Sedum acre* L., *S. reflexum* L. (possibly naturalized) and the fern *Polypodium vulgare* L.; the wall is shaded at one end by *Acer pseudoplatanus* L., *Corylus avellana* L. and *Crataegus monogyna* Jacquin. This shading is dense enough for *Campanula trachelium* L. to grow in the lane cutting. Tall herbage is developed on the south (lane) side of the wall, but on the field side there is short turf and the wall consists of moss-covered stones. The garden wall is also mossy and supports a variety of *Sedum* spp.

*L. sempronii* is present in small numbers (12 living and approximately 70 dead adult and juvenile shells seen in four examinations) along the top of the field wall for most of its length of 60 metres, under *Sedum acre*, among dead *Acer* leaves, and under the less dense areas of ivy. The cover varies from open to shaded. Two fresh dead shells of *L. sempronii* were found in moss on the field side of the garden wall, and dead shells indicate that it must occur at times on the sides of the field wall. The species is accompanied throughout by *Lauria cylindracea* (as in fossil occurrences in S.E. England) and is generally outnumbered by it. Except on the garden wall, *Vertigo pusilla* is also present, especially among dried leaves under ivy; *Vallonia costata* occurs on the more shaded 30 m of field wall top, and *Pyramidula rupestris* where it is more open and less thickly vegetated. The other molluscs recorded were *Cochlicopa lubrica*, *Ena obscura* (dead shell), *Discus rotundatus*, *Clausilia bidentata*, *Vitrina pellucida*, *Oxychilus alliarius*, *Aegopinella pura*, *Ceriuella virgata* (on more open part), *Candidula intersecta*, *Trichia striolata*, *T. hispida* (wall base only), *Cepea nemoralis* (few), *C. hortensis* (numerous), *Arianta arbustorum* (a few on the lane side of the wall) and *Helix aspersa*.

Nearby walls in better repair were searched to determine the extent of the colony. No further *L. sempronii* were found, but *V. pusilla* extends uphill for about 100 m along a flat-topped wall on the same side of the lane as the *L. sempronii* site, again being especially common under ivy. Slightly unexpected finds were a not-quite bleached shell of *Helicogona lapicida* on top of a front garden wall about 50 m from the colony, and a dead shell of *Oxyloma pfeifferi* at the base of the wall with *V. pusilla*.

Although the site is very near gardens, on balance it seems unlikely that *L. sempronii* is a recent introduction here. All the adult shells seen match both English fossil examples (*J. Conch., Lond.* **24** (1957) p. 190) and the Haresfield specimens in being edentulate (= var. *dilucida* Rossmässler). Furthermore the associated mollusca (especially *V. pusilla*) are typical of old walls and rocks, and finds of dead shells indicate that, if anything, *L. sempronii* was commonest in the past at the shaded end of the wall away from the cottages. At the same time nothing has emerged to indicate why *L. sempronii* lives at this particular site, where it is on occasion elusive. Other apparently suitable walls have been examined during 1985 and Haresfield Beacon was revisited, where the flat-topped drystone walls are more soil covered than at the new site; they may not have been in 1894. Collections by C. Upton and E. P. Blackburn in Gloucester City Museum were examined, but found to contain no specimens of *L. sempronii*.

The new site is now the subject of a Protected Site Agreement between the landowner and the Gloucestershire Trust for Nature Conservation Limited. Four full-grown and four juvenile shells have been deposited with the British Museum (Natural History) as voucher specimens.

I would like to thank Dr. M. P. Kerney for commenting on this note in draft, the land owner for allowing access to the site and so readily agreeing to the Protected Site Agreement, Mr. David Dartnell for access to the Gloucester City Museum collections, and Mrs Ruth Briggs of the Nature Conservancy Council and Mr Peter Bullard of GTNC for advice on potential conservation measures.

D. C. LONG  
20 Hall Rd., Leckhampton, Cheltenham, Glos., GL53 0HE  
(Received, 27 November 1985)

### CORRECTION

Plates 9 and 10 of *J. Conch. Lond.*, **32**, pp. 71–95 (1985), T. E. Thompson, G. M. Jarman and A. Zenetos, *Infralittoral macrobenthos of the Patras Gulf and Ionian Sea: opisthobranch molluscs*, have been accidentally transposed.



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**Junior Membership Officer in Charge:** Dr. R. C. PREECE, Godwin Laboratory, Free School Lane,  
Cambridge CB2 3RS.

**Newsletter Editor:** P. E. NEGUS, 30 Fleetwood Gardens, Market Harborough, Leicestershire  
LE16 9LX.

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# THE MOLLUSCS OF THE RIVER GREAT OUSE IN BEDFORDSHIRE

E. B. RANDS<sup>1</sup>

*(Presidential Address, delivered before the Society, 22nd March 1986)*

*Abstract:* Field work has been carried out in Bedfordshire since 1975 throughout the County. No accounts of the molluscs in the River Great Ouse have been published and this is an attempt to rationalise the situation. Brief historical accounts are given of the river itself together with habitat information for all the molluscs so far known to live in the River.

## INTRODUCTION

The River Great Ouse rises near Brackley in the calcareous limestone uplands of Northamptonshire. It then meanders across Buckinghamshire and enters Bedfordshire just west of Turvey at Newton Blossomville. The river then follows the County boundary between Beds. & Bucks. for several miles to Snelson Farm when it changes course eastwards and finally leaves the county near Eaton Socon.

At Brackley the river is an insignificant little brook and great difficulty was experienced in determining where the actual source began. However by the time the river reaches Kings Lynn and the Wash it has travelled approx. 160 miles about 45 miles through Bedfordshire. If the river flew like a bird across Bedfordshire the journey would be approximately 18 miles but because of the meandering nature of the river if a fish swam the whole length it would cover nearly 45 miles, as it cuts its channel through the Oxford Clay of north Bedfordshire. On either side of the present river course lay extensive beds of river gravels, which have been largely exploited by man during this century. Many of the holes left behind after the removal of the gravel have flooded and provide deep water habitats along the river system. These provide an extra dimension for the survival of many river organisms at times when dredging operations form a grave hazard for all life in a river.

There are 12 major bridges across the River Great Ouse in Bedfordshire plus a few small pedestrian ones. It is interesting to note that many of these were formerly fords. As late as 1818 the river at Felmersham was crossed by a ford. The bridge originally built there in 1818 was swept away by high flood water in 1819 and again in 1823. The present bridge is perhaps more substantial and has a long causeway extending northwards and in time of flood one can readily see why it is necessary. Bedford town itself originally had a ford, Batts Ford, and this was the only means of crossing the Ouse in this market town in the middle ages. More recently there was a ford at Kempston, with a footbridge as well. The ford was deepened in the late 1970's by the dredging operations of the Anglian Water Authority.

Harrold Bridge, Felmersham Bridge and Radwell Bridge all have long causeways leading up to the bridge itself, while Bromham Bridge and Turvey bridge incorporate a sort of causeway by extending the bridges across the flood meadows.

All the bridges were privately maintained until the 19th century. The bridge at Turvey was declared a 'County' bridge in 1881. Previously it had been maintained by the landlords

<sup>1</sup> 51 Wychwood Avenue, Luton, Bedfordshire LU2 7HT.



of the parish, originally the Mordaunts and then the Higgins family, plus contributions from the parishioners. As long ago as 1510 a Mr. Harry Hanson left 20 pence in his will toward the upkeep of the bridge. As the bridge passes over the county boundary the responsibility for its upkeep passed to the Buckinghamshire parishioners. As there is no sign of anyone living within sight of the bridge in Bucks one wonders who paid for its upkeep.

Although nothing substantial has been published about the River Great Ouse and its animal life, it has long been known to be one of the richest rivers in the British Isles for invertebrates and especially molluscs. Despite all the 'improvement schemes' or 'despoilments' carried out by man in the name of progress the diversity of molluscan life is still very high. Rising, as it does, in a calcareous habitat, the river carries with it many minerals and salts which are cut out of the banks as the river continues to modify its course. It is not therefore too surprising to find that the checklist of molluscs known to live in the River Great Ouse is so long.

To be able to sample the potential of the river one must have access points. Over most of the length of the river in Bedfordshire access is very difficult and the number of bridges that span the river do give one an access point. It is usually feasible to scramble down the banks beside the bridges and very often there is a small area of flattened land where others have done the same thing. Also around the base of bridge piers is a good spot to look for accumulations of flood debris, sometimes extremely rich in mollusc shells. Searches along the length of causeway piers also yield areas where flood debris will be caught up and accumulate. When dealing with shells from flood debris care must be taken to note how old the shells are. Some will be very old and worn and indeed may be from fossil deposits, while others may have been swept down on the flood tide for a long distance. Many land shells may be present and must not be confused with the true inhabitants of the river.

#### ANNOTATED LIST OF MOLLUSCA

##### **Theodoxus fluviatilis** (L)

First VC30 record, first R. Ouse record, 1889, Rev. Carleton Greene at Great Barford. Common, especially upstream from Bedford. River bed species often found attached to mussels. Very common in flood debris, both dead and alive.

##### **Viviparus viviparus** (L)

First VC30 record, first R. Ouse record, 1968 at Kempston by E. B. Rands. Fairly common in association with *V. contectus*. Juveniles common in flood debris.

##### **Viviparus contectus** (Millet)

Fi. VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford. More common than *V. viviparus*. Common in flood debris.

##### **Valvata cristata** Müller

First VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford. Very common in R. Ouse but often overlooked because of its small size. Very common in fine flood debris.

##### **Valvata piscinalis** (Müller)

First VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford. Locally very common and usually in fast running stretches. Can be the commonest shell in some batches of flood debris.



**Potamopyrgus jenkinsi** (Smith)

First VC30 record, first R. Ouse record, 1940, J. E. Cooper at Goldington.

Very common everywhere in the R. Ouse and it is surprising that it wasn't found in VC30 until 1940. Very common in flood debris. Keeled and unkeeled specimens present.

**Bithynia tentaculata** (L)

First VC30 record, 1884, J. Saunders at Limbury, first R. Ouse record, 1889, Rev. Carleton Greene, Great Barford.

Very common all along R. Ouse. Care must be taken with juveniles as they can be confused with *B. leachii*. Very common in flood debris, both dead and alive.

**Bithynia leachii** (Sheppard)

First VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford.

Nearly as common as previous species but prefers thickly vegetated stretches of the R. Ouse. Very common in flood debris and great care must be taken to separate this species from juveniles of *B. tentaculata*.

**Physa fontinalis** (L)

First VC30 record, 1886, J. Saunders, Near Luton, first R. Ouse record, 1945 B. Verdcourt.

Local along R. Ouse but the shell is so fragile that it fragments quickly on the death of the animal and may be more common than is thought. Very seldom found intact in shell debris but occasionally shell fragments can be recognised.

**Physa cf acuta** Draparnaud

Specimens resembling this species are common in the R. Ouse but there is great confusion about the taxonomy of this genus worldwide. The shells of this species are very robust and are fairly common in flood debris.

**Lymnaea truncatula** (Müller)

First VC30 record, first R. Ouse record, 1886, J. W. Wood, Bedford.

Locally common along the R. Ouse, showing preference for shallow margins and ditches entering the Ouse system. Not found in deep water. Very common in flood debris.

**Lymnaea palustris** (Müller)

First VC30 record, 1886, J. Saunders at Biscot, first R. Ouse record, 1945, B. Verdcourt.

Not commonly found but this may be due to seasonal fluctuations. This species may be present in vast numbers on one day and be totally missing (apparently) within hours. One or two specimens usually present in flood debris but never in great numbers.

**Lymnaea stagnalis** (L)

First VC30 record, 1884, J. Saunders at Limbury, first R. Ouse record not known.

Very common especially where there is floating vegetation. The snails can often be watched travelling upside down across the surface of the river between water lily leaves. Flood debris usually contains specimens of varying ages in considerable quantity.

**Lymnaea auricularia** (L)

First VC30 record, 1884, J. Saunders at Luton Hoo, first R. Ouse record, 1889, Rev. Carleton Greene, Great Barford.

Common locally throughout the R. Ouse. Found in most flood debris samples, occasionally in large numbers.

**Lymnaea peregra** (Müller)

First VC30 record, 1884, J. Saunders at Biscot, first R. Ouse record, 1889, Rev. Carleton Greene, Great Barford.

Probably the commonest mollusc in the R. Ouse and in flood debris. Many different forms and sizes found.

**Planorbis planorbis** (L)

First VC30 record, 1884, J. Saunders at Biscot, first R. Ouse record not known.

Fairly common all along the R. Ouse in low densities. This species appears to hybridise with *P. carinatus* and intermediate specimens can pose difficulties. Care should be taken to obtain positive specimens in each case. A common species in flood debris.

**Planorbis carinatus** Müller

First VC30 record, 1889, J. Saunders in River Ivel, first R. Ouse record, 1945, B. Verdcourt.

More common than *P. planorbis* but many hybrids can be confusing. As with previous species care is needed. Very common in flood debris.

**Anisus leucostoma** (Millet)

First VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford.

Locally common along the R. Ouse. When present in flood debris it is very abundant. Prefers backwaters with mud.

**Anisus vortex** (L)

First VC30 record, 1887, J. Saunders at Limbury, first R. Ouse record not known.

Fairly common usually not with *A. leucostoma*. Prefers flowing water with plenty of weed. When present in flood debris it is usually common.

**Bathyomphalus contortus** (L)

First VC30 record, 1886, J. Saunders from Luton Hoo Park, first R. Ouse record not known.

Very common in the R. Ouse throughout Bedfordshire. Present in all habitats, shows no preference between running or standing water or between clean or muddy water. Very common in flood debris.

**Gyraulus albus** (Müller)

First VC30 record, first R. Ouse record, 1886, J. W. Wood from Bedford.

Very common throughout the R. Ouse. Care should be taken to examine specimens carefully in case *Gyraulus laevis* should be present as it is in Wyboston Gravel Pits which are immediately adjacent to the R. Ouse. Common in flood debris.

**Armiger crista** (L)

First VC30 record, 1886, J. Saunders at Kitchin End, first R. Ouse record not known.

This very small species is undoubtedly overlooked in the field. Locally abundant when found on plants in still or running water. It will tolerate stagnant water and in some cases occurs in great abundance with *Pisidium obtusale* and *P. personatum*. Found in most flood debris samples, its form varying from smooth to the very ridged nautilus form.

**Hippeutis complanatus** (L)

First VC30 record, 1887, J. Saunders at Limbury, first R. Ouse record not known.

Not abundant anywhere in the R. Ouse. It favours slow water with good weed growth and can be found grazing on the underside of leaves. Fairly frequent in flood debris in small numbers.

**Planorbarius corneus** (L)

First VC30 record, 1885, J. Saunders at Limbury, first R. Ouse record, 1889, Rev. Carleton Greene, Great Barford.

Generally distributed throughout the R. Ouse in Bedfordshire. Likes good weed growth and standing water. Fairly common in flood debris, especially juvenile shells.

**Ancylus fluviatilis** Müller

First VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford.

Present where there is running water over stones. Present in large numbers at sites of weirs or at the outflow side of locks. Flood debris collected near these usually have a large number of these fresh water limpets present.

**Ferrissia wautieri** (Mirolli)

First VC30 record, first R. Ouse record, 1978, R. D. Wilmot, Great Barford.

The Vice County record for this small freshwater limpet rests on one dead shell dredged from the R. Ouse at Great Barford on the 18 April 1978. Dr. R. Preece examined the molluscs obtained during the dredging and found only one shell. Other samples obtained from the R. Ouse during the same operation yielded no further specimens.

**Acroloxus lacustris** (L)

First VC30 record, 1888, J. Saunders at Limbury, first R. Ouse record not known.

This freshwater limpet is not common anywhere in the R. Ouse. It lives on the stems and leaves of water plants in still, undisturbed parts of the river. The habitat for this species has been rapidly diminishing during the last decade. Shells are found infrequently in flood debris. Unless river management policies alter this species will continue to decline in the R. Ouse.

**Unio pictorum** (L)

First VC30 record, first R. Ouse record, 1886, J. W. Wood at Bedford.

Very common in the R. Ouse and can be obtained fairly easily alive with a net fishing from the banks. It is a common species in flood debris, especially on a slow bend of the river where large freshwater mussels are obtain thrown up in large deposits. Freshwater mussels are often found on the middens of water voles, where the anterior end of the two valves is chopped off by the vole in order to extract the animal.

**Unio tumidus** Phillipsson

First VC30 record, first R. Ouse record, 1886, J. W. Wood from Bedford.

Fairly common in the R. Ouse especially in the upper reaches above Bedford. Co-habits with *Unio Pictourum* but cannot be mistaken for it as the specimens are particularly tumid and much taller than *U. Pictorum*. The juveniles are usually highly coloured in green and yellow. Very common in flood debris.

**Anodonta cygnea** (L)

First VC30 record, 1885, J. Saunders from Luton Hoo, first R. Ouse record, 1889, Rev. Carleton Greene, Great Barford.

This species used to be more common in the early 1970's than it appears to be to-day. Drastic deep dredging operations seem to have affected this species very severely. It is hoped that it will gradually build up in numbers again if dredging operations are not carried out too often. The proposed 8–10 year cycle of the Anglian Water Authority would not give these mussels a long enough, undisturbed period in which to build up large numbers. Very few found in flood debris.

**Anodonta anatina** (L)

First VC30 record, first R. Ouse record, 1916, E. D. Marquand at Bedford.

Very common in the R. Ouse and does not appear to have been as badly affected by dredging operations as the previous species. Can be present in very large numbers, with many juveniles present. Very common in flood debris.

**Pseudanodonta complanata** (Rossmässler)

First VC30 record, first R. Ouse record, 1940, J. E. Cooper from Kempston.

Found mainly in the upper reaches of the R. Ouse above Bedford. This species favours



deep, clean water and is seldom reached by netting from the bank, except after very high flood conditions when they are swept by the current towards bays in the banks. As the level of the water goes down the mussels channel their way back to the middle of the channel. Dead, fresh valves often found in flood debris.

**Sphaerium corneum** (L)

First VC30 record, 1884, J. Saunders at Limbury, first R. Ouse record, 1889, Rev. Carleton Greene, Great Barford.

Very common throughout the R. Ouse. It is almost impossible to fish for molluscs in the river without finding this species. Very common in flood debris.

**Sphaerium rivicola** (Lamarck)

First VC30 record, first R. Ouse record, 1948, B. Verdcourt from Bedford.

This record is based on one juvenile shell found in the river at Bedford by B. Verdcourt and determined by A. E. Ellis. This species favours deep water habitats but it is surprising that no further specimens have been found either alive or in flood debris. The shells of this species are so distinctive that a good field worker could not mistake it for any of the other *Sphaerium spp.* It is found quite commonly in the Grand Union Canal which passes very close to the R. Ouse in its upper reaches which makes its absence even more puzzling.

**Sphaerium lacustre** (Müller)

First VC30 record, 1887, J. Saunders at Limbury, first R. Ouse record not known.

Locally fairly common. Requires slow running water and weed roots. The habitat is not common any more in the R. Ouse and this species will probably decline in the river itself and perhaps move into side ditches and gravel pits as more of its habitat disappears in dredging operations. Infrequently found in flood debris.

**Pisidium amnicum** (Müller)

First VC30 record, first R. Ouse record, 1916, E. D. Marquand at Bedford.

Fairly common throughout the R. Ouse in Bedfordshire. It is the largest of our British *Pisidium spp.* and cannot be confused with any other. Fairly common in flood debris.

**Pisidium casertanum** (Poli)

First VC30 record, first R. Ouse record, 1918, C. Oldham at Bromham.

Common in R. Ouse. Appears to have no habitat preference and several forms do occur. Common in flood debris.

**Pisidium personatum** Malm

First VC30 record, first R. Ouse record, 1923, C. Oldham at Turvey.

A local species showing a marked preference for polluted spots along the river where very few other molluscs are found. Dirty outflows and cattle drinking areas seem to be favoured. Local in flood debris.

**Pisidium obtusale** (Lamarck)

First VC30 record, 1887, J. Saunders at Limbury, first R. Ouse record, 1940, J. E. Cooper at Bedford.

Very few records for this species. It's habitat preference is even worse than the previous species. Very few in flood debris.

**Pisidium milium** Held

First VC30 record, 1884, J. Saunders at Limbury, first R. Ouse record, 1918, C. Oldham at Bromham.

A local species which likes a clean muddy substrate. When present it can be very plentiful especially in flood debris.

**Pisidium subtruncatum** Malm

First VC30 record, first R. Ouse record, 1918, C. Oldham at Bromham.

Very common species occurring in almost any habitat. Common in flood debris.

**Pisidium supinum** Schmidt

First VC30 record, first R. Ouse record, 1918, C. Oldham at Bromham.

Locally common throughout the R. Ouse where the bottom is muddy but clean and the flow of water fairly fast. Fairly common in flood debris but may have travelled a fair distance in the fast current.

**Pisidium henslowanum** (Sheppard)

First VC30 record, first R. Ouse record, 1886, J. W. Wood at Bedford.

Fairly common throughout the R. Ouse in Bedfordshire. It likes swift flowing water and is usually a deep water species. Fairly common in flood debris.

**Pisidium hibernicum** Westerlund

Very local species which is surprising as it tolerates most habitats. Occasionally found in flood debris.

**Pisidium nitidum** Jenyns

First VC30 record, first R. Ouse record, 1918, C. Oldham at Bromham.

Very common throughout the R. Ouse. Common in flood debris.

**Pisidium pulchellum** Jenyns

First VC30 record, first R. Ouse record, 1984, A. J. Rundle & D. W. Guntrip at Radwell.

This Vice County record is based on dead valves found in flood debris at Radwell during an intensive survey into a small habitat beside the bridge. No living specimens were found but several fairly fresh dead shells. In 1985 living specimens were found in the River Ouzel in the South of Bedfordshire.

**Pisidium moitessierianum** Paladilhe

First VC30 record, first R. Ouse record, 1918, C. Oldham at Bromham.

This is one of the smallest *Pisidium spp.* and can be overlooked because of its size. It is very common in the higher reaches of the R. Ouse above Bedford. It is sometimes the commonest *Pisidium spp.* present in flood debris.

**Pisidium tenuilineatum** Stelfox

First VC30 record, first R. Ouse record, 1968, M. P. Kerney at Bromham.

The Vice County record for this species rests on one dead valve found at Bromham. In 1984 several dead valves were found in flood debris at Radwell so that it is possible that live specimens may turn up with careful searching. This is the smallest *Pisidium spp.* and a very fine mesh net would be needed to find them in their living habitat.

**Dreissena polymorpha** (Pallas)

First VC30 record, first R. Ouse record, 1911, E. D. Marquand at Bedford.

This used to be a very common species in the R. Ouse in Bedfordshire. At Oakley Bridge in the early 1970's no stone, boulder or even Freshwater Mussel could be found without several specimens clinging to it. Since the re-organisation of the river by the Anglian Water Authority the channel has been deepened, the river widened, the bottom substrate removed and the whole character of stretches of river changed. The habitat for the Zebra mussel has been literally removed and the mussels now have to rely on bridge piers for their support. Flood debris still has a large number of shells present but they are nearly always dead shells. However the many flooded gravel pits along the R. Ouse seem to be offering a new habitat for *Dreissena polymorpha*. Much rubbish, in the form of old cars, bicycles, cans etc. is thrown into these pits and the mussels are making good use of this man-made rubbish tip habitat.

ACKNOWLEDGEMENT

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# BIOLOGICAL SPECIES-LIMITS AND SYSTEMATICS OF THE CLAUSILIIDAE (GASTROPODA) OF THE MALTESE ISLANDS

D. T. HOLYOAK<sup>1</sup>

(Accepted for publication, 16th May 1985)

*Abstract:* Eight forms of Clausiliidae (Alopiini) are recognised from the Maltese archipelago and Lampedusa. Characters of their shells and distal genitalia are discussed. The distribution of all of the forms is essentially allopatric. Hybridisation usually occurs where ranges of different forms meet; in some cases hybrids are rare, but in others entire local populations are of hybrid origin. Based mainly on evidence of the extent of reproductive isolation, the seven forms in the Maltese Islands are classified into two biological species (*syracusana* and *imitatrix*). From evidence of their affinity it is suggested that these should be placed together in the genus *Lampedusa*, along with *lopadusae* from the Island of Lampedusa.

## INTRODUCTION

The distribution and biogeographical history of the Clausiliidae of the Maltese Islands have been studied in detail by Mr. Martin Thake (1985). From the detailed distributional information he obtained it became clear that current systematic treatments (Soós 1933, Nordsieck 1979) are inadequate. Thus, in 1983 I was asked to collaborate in anatomical and conchological examination of material he had collected with the intention of revising the systematics. The present paper gives the results of this study along with a summary of Mr. Thake's distributional data.

Two tribes of the clausiliid subfamily Alopiinae are represented in Malta (Nordsieck 1979), the Alopiini and the Cochlodini. In the Maltese islands the Cochlodini has only one species, *Papillifera papillaris* (O. F. Müller, 1774). This species also occurs in southern France and Italy and because it apparently does not pose taxonomic problems it is not discussed further here.

The most detailed account of the Maltese Alopiini was by Soós (1933). Zilch (1977) gave a revised generic classification and this was used by Nordsieck (1979) with minor amendments. The arrangements adopted by these authors are summarised in Table 1.

The present revision considers conchological and anatomical characters in turn before describing the essentially allopatric patterns of distribution of each form. Species-limits are then deduced from evidence of hybridisation where ranges of different forms meet. Finally suggestions are made for a generic classification and a list of the forms and synonyms is given.

## SHELL CHARACTERS

Shells of all forms may be distinguished by characters given in the following key and from the photographs in Plates 21 and 22.

<sup>1</sup> Department of Geography, University of Nottingham, University Park, Nottingham, NG7 2RD, U.K.

*Key to shells of Clausiliidae from the Maltese archipelago and nearby islands:*

1. Shell almost smooth: sutural papillae present *Papillifera papillaris*  
 Shell with closely or widely spaced ribs; sutural papillae absent 2.
2. Shell apex normally decollated; two or three palatal folds present; lunella dorsal 3.  
 Shell apex normally not decollated; palatal folds one or nil; lunella subdorsal 6.
3. Shell very wide in relation to height, typically 9–12 mm high  $\times$  4–5.5 mm wide  
 (Gozo; local) *mamotica*  
 Shell less ventricose 4.
4. Shell somewhat scalariform, giving markedly turreted appearance to whorls  
 (Malta; local) *scalaris*  
 Shell not scalariform; whorls not appearing turreted 5.
5. Ribs closely spaced (100–140 on penultimate whorl); shell more ventricose *oscitans*  
 Ribs widely spaced (40–50 on penultimate whorl); shell less ventricose *syracusana*  
 (Populations intermediate between *oscitans* and *syracusana* are not uncommon).
6. Back of body whorl with twenty or more rather evenly spaced ribs; one sutural fold;  
 peristome markedly thickened (Lampedusa only) *lopadusae*  
 Back of body whorl with fewer than fifteen ribs that are often unevenly spaced; no  
 sutural fold; peristome thickened or unthickened (Malta and Filfla only) 7.
7. Back of body whorl with 0 or 1 short ribs (i.e. ribs extending only a short distance from  
 suture); columellar fold most often rather low, so that sinus between columellar and  
 parietal folds appears shallow; body whorl only slightly narrower than penultimate  
 whorl and not tapering downwards (Malta: rare) *melitensis*  
 Back of body whorl with 2 or more short ribs; columellar fold often higher, usually  
 giving a definite and partly enclosed sinus between columellar and parietal folds; body  
 whorl distinctly narrower than penultimate whorl and tapering downwards 8.
8. Ribbing on penultimate whorl and spire of shell usually slightly finer (other  
 conchological differences are inconstant) (Filfla only) *gattoi*  
 Ribbing on penultimate whorl and spire of shell usually coarser (Malta) *imitatrix*  
 Localised forms occur with shells intermediate between *imitatrix* and *oscitans*, between  
*melitensis* and *oscitans*, perhaps between *imitatrix* and *syracusana*, and between *syracusana*  
 and *scalaris*. These are evidently hybrids; their characters and significance are  
 considered below.

## ANATOMICAL CHARACTERS

Soós (1933) described and figured the genitalia of seven of the eight forms listed in Table 1 (all except *imitatrix*). He found only minor differences between forms and some of these might be due to individual variability.

In the present study over half of the specimens dissected were found to have small and evidently immature genitalia despite the fact that their shells had a mature peristome. Distal genitalia were studied in *imitatrix* (3 specimens, 2 of them fully adult); *melitensis* (2 specimens, both fully adult), *syracusana* (11, 3), *oscitans* (8, 4), *scalaris* (3, 0) and *mamotica* (5, 0).

The adult genitalia of *imitatrix* and *melitensis* differed from those of the other forms in having the appendix on the penis shorter and stouter. In addition these two forms typically

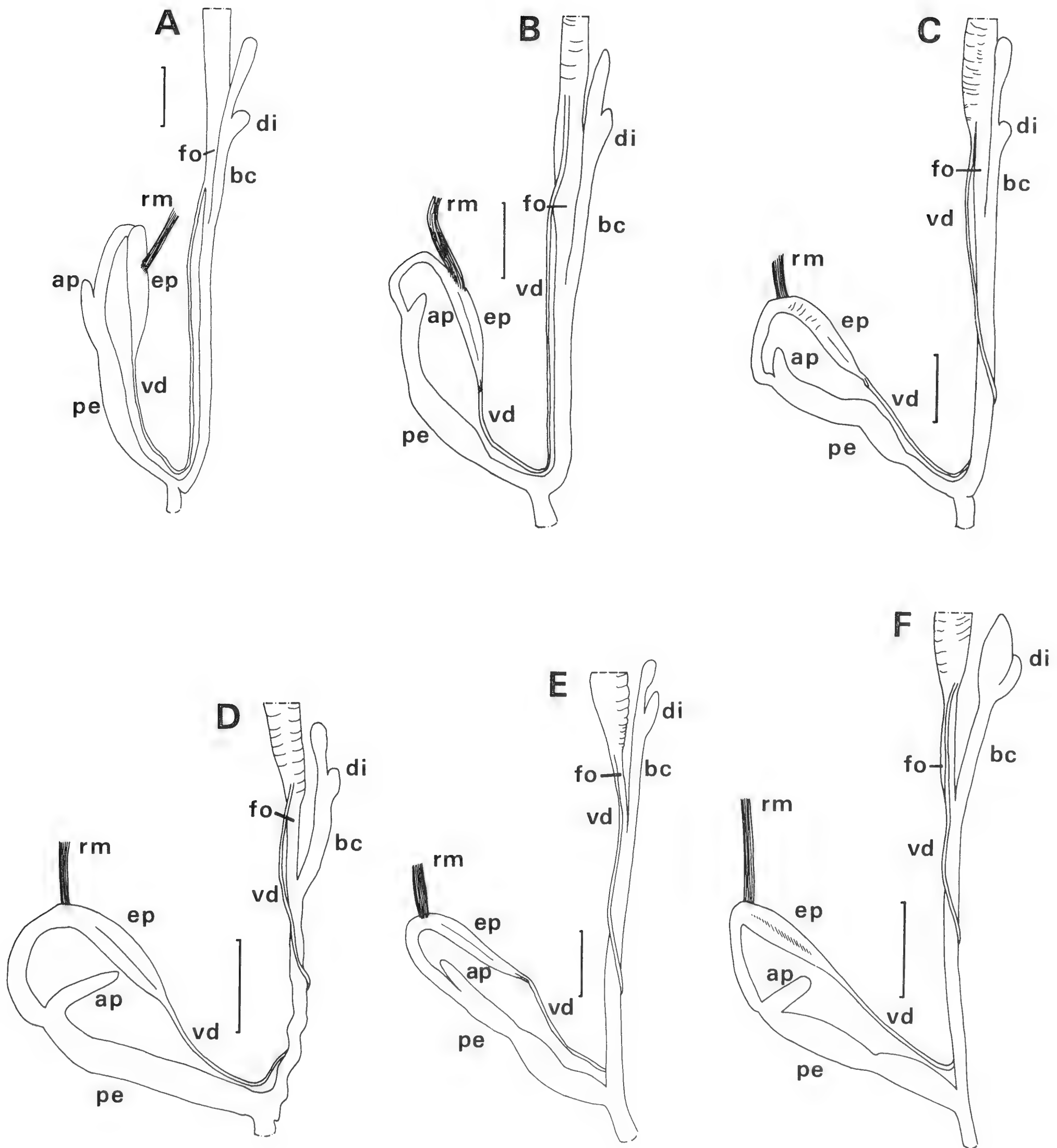


Fig. 1. Distal genitalia of Maltese Clausiliidae.

A, B *imitatrix* (lower Wied Gerzuma, western Malta); C *melitensis* (Rdum il Madliena, south-western Malta); D *oscitans* (1½ miles NW. of Rabat, Malta); E, F *syracusana* (1½ miles NW. of Rabat, Malta).

All specimens were collected by Martin Thake in 1983; they are now in Colln. D. T. Holyoak & M. B. Seddon. All scale bars = 1.0 mm.

ap penial appendix, bc bursa copulatrix, di diverticulum, ep epiphallus, fo free oviduct, pe penis, rm retractor muscle, vd vas deferens.



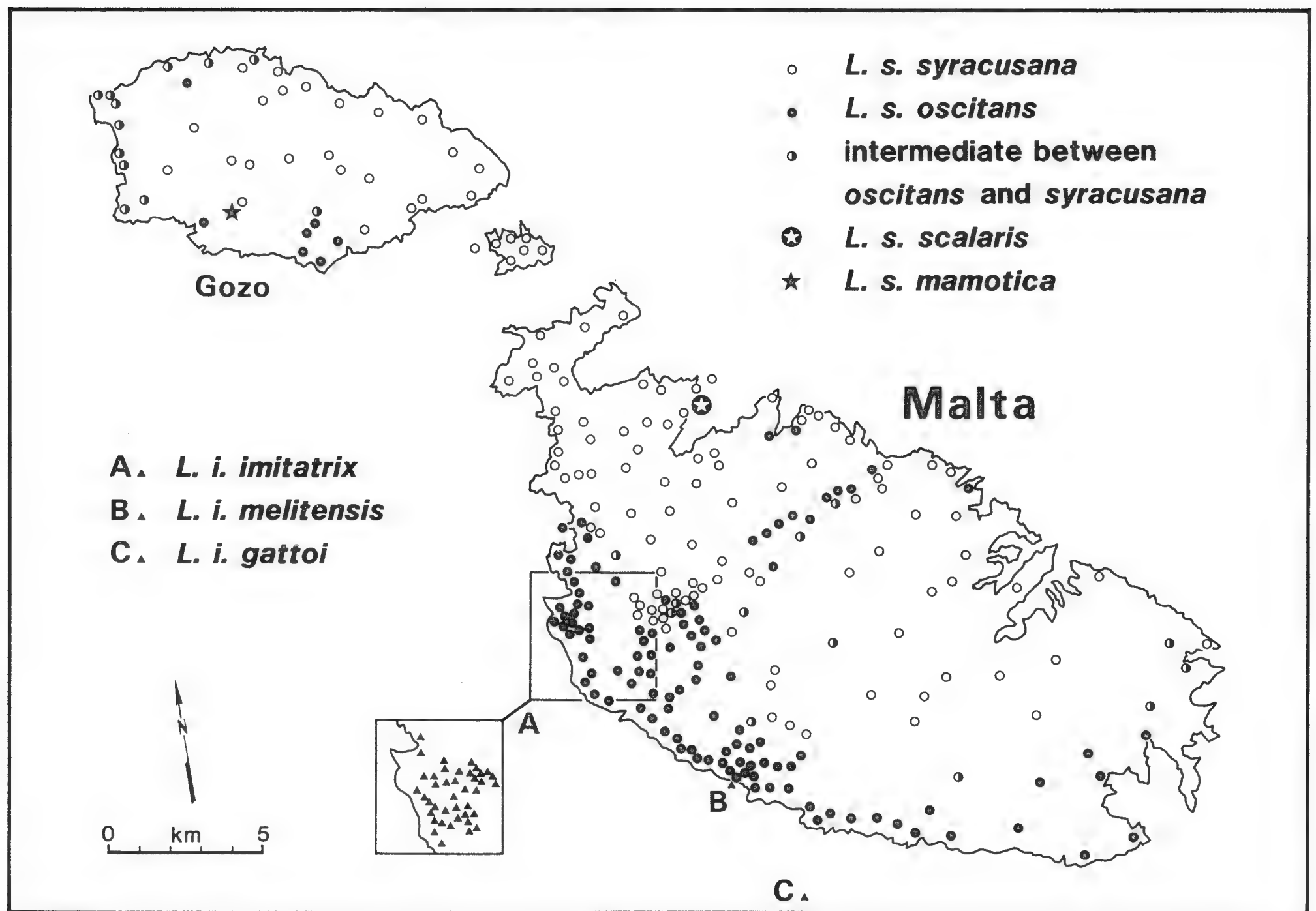


Fig. 2. Distribution of genus *Lampedusa* (Clausiliidae) in the Maltese islands (based on studies by Martin Thake (1985 and in litt.)).

had the diverticulum of the bursa copulatrix inserted further from the proximal end. Fig. 1 gives drawings of representative dissections to illustrate these differences.

The drawings of *emersoniana* (= *imitatrix*) and *gattoi* given by Soós (1933) likewise show a smaller penial appendix than in the other forms, although that shown for *emersoniana* was longer than in the *imitatrix* dissected in the present study. However, the position of insertion of the diverticulum on the bursa copulatrix was more variable in the specimens Soós figured (it was low down for example in the specimen of *oscitans* shown in his Fig. 4). The genital anatomy of *lopadusae* is apparently known only from Soós' description and figure. He shows both the penis and penial appendix as somewhat longer and thinner than in any of the allied forms.

It may thus be possible to recognise three groups of forms on the basis of the relative size of the penial appendix: (1) *lopadusae*, with long appendix (length/diameter >10); (2) *syracusana*, *oscitans*, *scalaris* and *mamotica* with moderately long appendix (length/diameter 2.4–6); (3) *imitatrix*, *melitensis* and *gattoi* with short appendix (length/diameter 1.7–2). Study of larger samples will probably show overlapping ranges of variation in this character.

#### DISTRIBUTIONAL DATA

The forms with which we are concerned here are restricted to the Maltese archipelago, except that *lopadusae* is endemic on the small island of Lampedusa and *syracusana* occurs also near Syracuse on Sicily. Within the Maltese archipelago the distribution of all of the forms was studied in detail by Martin Thake (1985 and in litt.) and it is his data that is given in Fig. 2.

All of the Maltese forms have allopatric (i.e. non-overlapping) ranges. Two forms are widespread in the archipelago (*syracusana*, *oscitans*) and a third has a range several kilometres across (*imitatrix*). The other four are all restricted to single localities: on an offshore islet (*gattoi*), on south-western Malta (*melitensis*), on northern Malta (*scalaris*) and on southern Gozo (*mamotica*).

#### HYBRIDISATION AND THE LIMITS OF SPECIES

Martin Thake realised that shells of intermediate character found where ranges of two allopatric forms met were likely to be hybrids and thus important in elucidating the relationships of the different forms. Hence he searched energetically for such forms and collected intensively when he found them, taking pains to collect all shells from the critical sites not just the rare 'hybrids'. He also collected carefully at sites where two forms coexist at the edges of their ranges without occurrence of apparent 'hybrids'.

Thake (1985) has described occurrence of numerous and extensive zones of hybridisation between *syracusana* and *oscitans*. There can be little doubt that these populations with intermediate shell morphology (shape and rib number) are of hybrid origin (cf. Pl. 22, Figs. A–D). Thus at any one site only one form occurs, be it *syracusana*, *oscitans* or an intermediate type resembling one or the other of these more or less closely. My own data and those of Thake (*op. cit.*, Fig. 5) show that at closely adjacent sites the complete range of intermediate shell types sometimes occurs. Thake also showed that at some sites the zone of hybridisation was narrow; for example at Ghajn Znuber hybridisation occurred in a band as little as 50 m wide.

Hence it is clear that *syracusana* and *oscitans* hybridise freely wherever their ranges come into direct contact and that populations of such hybrid origin persist widely. Nonetheless, the relatively narrow hybrid zones suggest that hybrids may be at some disadvantage in comparison to the parental types, unless one of the forms is currently in the process of replacing the other. It is clear that *oscitans* and *syracusana* are far from having attained reproductive isolation, so they should be treated as conspecific. The conspicuous differences in shell form suggest it is useful however, to afford them subspecific status.

The form *scalaris* is close to *syracusana* in all characters except its attractively scalariform shell. A series of four population samples collected by Martin Thake at the eastern edge of the range of *scalaris* (northern shore of St. Paul's Bay) shows progressive reduction of the scalariform tendency over a distance of about 200 m. The 9 shells in the first of the samples are all typical *scalaris*, the 17 shells of the fourth sample are all typical *syracusana*, whereas the second and third samples from intermediate locations are composed entirely of intermediate shells (8 and 29 shells respectively) (see Pl. 22, Figs. E,F). Thus it appears that *scalaris* interbreeds freely with *syracusana* to form a hybrid zone where their ranges meet. Consequently it can be treated as a subspecies of *syracusana* if the consistently scalariform shell is thought important enough to merit nomenclatural separation of this local population.

A localised population on Gozo (*mamotica*) differs from *oscitans* only in having a remarkably ventricose shell (Pl. 22, Fig. G). The range of *mamotica* does not meet that of any other form so there is no natural test of its interfertility with other forms. Because of the general similarity of *mamotica* and *oscitans* it seems likely they are sufficiently closely related to be best regarded as conspecific. This impression of the best taxonomic treatment for *mamotica* may be strengthened by the wide variety of shell form evident within the assemblage (*syracusana* + *oscitans* + *scalaris*) that is known to be a single species from the evidence described above.

The three forms *imitatrix*, *melitensis* and *gattoi* stand somewhat apart from the other Maltese forms in shell and anatomical characters so they have often been placed in a separate genus (Table 1). The range of *imitatrix* meets the ranges of *syracusana* and *oscitans* (Fig. 2) and there is evidence that infrequent hybridisation occurs with both of these forms.

Random samples were collected from Tal Merhia by Martin Thake in November and December 1983, from the very small areas where *imitatrix* and *oscitans* overlap. Intermediate and presumably hybrid shells (Pl. 21, Fig. H) were rare. In sample O from an area measuring  $5 \times 4$  m the collection comprised 19 *imitatrix*, 27 *oscitans* and 2 hybrids. In sample P from 'a single boulder' were 15 *imitatrix*, 3 (dead shells) of *oscitans* and 2 hybrids. Samples from a series of adjacent, narrowly defined localities gave results as follows: Sample 2/2 had 4 *imitatrix* and 2 hybrids; Sample 2/3 had 6 *imitatrix* and 6 *oscitans*; Sample 2/4 had 4 *imitatrix* and 23 *oscitans*; Sample 2/5 had 5 *imitatrix* and 2 *oscitans*; Sample 2/6 had 10 *oscitans* and 1 hybrid; Sample 2/9 had 3 *imitatrix* and 21 *oscitans*; Sample 2/10 had 4 *imitatrix* and 3 *oscitans*; Sample 2/11 had 20 *imitatrix* and 1 hybrid.

Apparently a total of only about ten hybrids between *imitatrix* and *oscitans* has been identified so far. Populations comprised entirely of hybrids do not occur and it appears that at places where their ranges meet phenotypically normal *imitatrix* and *oscitans* outnumber the hybrids.

One possibility is that hybridisation is most likely to occur when one form is in a small minority at a site (so that it has difficulty finding the 'proper' mate). Another possibility is that mating occurs at random but reduced fecundity prevents appearance of many hybrids. Only a detailed observational or experimental study can test such hypotheses. However, it is clear from the rarity of hybrids and the narrowness of the hybrid zone that hybrids must be at a considerable selective disadvantage compared to the parental types. Thus it is appropriate to regard *imitatrix* and *oscitans* as separate species because they have almost achieved reproductive isolation. Repeated occurrence of hybrids suggests nonetheless that they are closely related genetically. Ecological similarities may also be important in preventing these two forms from coexisting.

The ranges of *imitatrix* and *syracusana* also meet locally (Fig. 2) and there is a possibility of rare hybridisation occurring. Because they are coarsely ribbed the shells of these two forms are (superficially) more similar to each other than are those of *imitatrix* and *oscitans*, so hybridisation is much more difficult to detect. Two shells from rocks in the uppermost reaches of Santi valley do, however, show intermediate characters (e.g. Pl. 21, Fig. G). They were collected with 43 *imitatrix* and 2 *syracusana* at the point where their ranges abut, so their hybrid origin is probable. Hybrids between these forms are certainly rare; as with the *imitatrix*  $\times$  *syracusana* hybrids they suggest that reproductive isolation has almost but not quite been attained. Likewise, they thus imply *imitatrix* and *oscitans* are different species that are genetically fairly closely related.

The range of the rare form *melitensis* meets that of *oscitans* in one place, where two hybrids have been collected (Pl. 22, Fig. H). Because of the rarity of *melitensis* large collections were not made because these could have caused its extinction. The form on the islet of Filfla (*gattoi*) is isolated from other Clausiliidae.

Both *melitensis* and *gattoi* are close to *imitatrix* in shell and anatomical characters. If these similarities imply close relationships then it is best to treat them as conspecific with *imitatrix*.

The form isolated on the island of Lampedusa (*lopadusae*) differs sharply from other forms in shell characters and there is apparently a small anatomical difference. This form is thus more conveniently treated as a distinct species than as conspecific with any of the Maltese forms.



# GENERIC CLASSIFICATION

Whereas the limits of species can often be objectively defined by evidence of infertility the limits of genera are largely a matter of convenience and convention. Pintér (1977, p. 224) was eloquent in deploring the recent trend towards multiplication of generic names on the basis of small anatomical differences: ‘Auf die Gefahr der “Nouvelle École” des vorigen Jahrhunderts kann nie oft genug hingewiesen werden. Man spricht heute bereits von einem “anatomischen Bourguignatismus.”’

Recent classifications of the Clausiliidae have tended to use large numbers of narrowly defined genera and subgenera, as for instance when the Maltese forms that are the subject of this paper were placed in two genera (one with two subgenera) by Zilch (1977) and Nordsieck (1979). It is argued above that just three fairly closely related species are involved, so such a subdivision into monotypic genera and subgenera is unnecessary. It is indeed undesirable as use of superfluous subgenera may lead to cumbersome quadrinomials. *Lampedusa* is the earliest generic name for this group; its synonymy is listed below.

## LIST OF FORMS AND SYNONYMS

The list below gives the valid name for each taxon in accordance with the evidence of species-limits described above. In addition synonyms of genus-group and species-group names are listed, including orthographic variants. However, no attempt has been made to list the many different combinations of genus-group and species-group names contained in the literature (cf. Table 1). The range of each form is also listed briefly.

Genus **Lampedusa** O. Boettger, 1877

Synonyms: *Mauritanica* O. Boettger, 1877 (part); *Imitatrix* Westerlund, 1884; *Lamellifera* Monterosato, 1893 (not Westerlund, 1890); *Lopadusaria* Monterosato, 1893; *Lopedusaria* Westerlund, 1901; *Priodelima* A. J. Wagner, 1925 (part); *Muticaria* Lindholm, 1925.

**Lampedusa lopadusae** (Calcara, 1846)

Based on: *Clausilia lopadusae* Calcara, 1846;

Synonyms: *Clausilia lopedusae* L. Pfeiffer, 1848; *Clausilia lampedosae* Charpentier, 1852; *Clausilia lampedusae* Rossmässler, 1859; *Clausilia lopedusae* var. *pallidescens* A. Schmidt, 1868; *Clausilia solidula* Monterosato, 1893; *Clausilia nodulosa* Monterosato, 1893;

Range: Lampedusa and Lampione.

**Lampedusa imitatrix** (O. Boettger, 1879)

**L. i. imitatrix**

Based on *Clausilia imitatrix* O. Boettger, 1879;

Synonym: *Clausilia emersoniana* Pilsbry, 1913;

Range: western Malta.

**L. i. melitensis** (Caruana-Gatto, 1892)

Based on: *Clausilia (Papillifera) melitensis* Caruana-Gatto, 1892;

Range: western Malta (very local, near coast opposite Filfla).

**L. i. gattoi** Soós, 1933

Based on: *Lampedusa (Imitatrix) Gattoi* Soós, 1933;



TABLE 1  
Recent classifications of *Lampedusa* (Clausiliidae).

TAXON	SOÓS 1933	ZILCH 1977	NORDSIECK 1979	THIS PAPER
<i>Clausilia lopadusae</i> Calcara, 1846	<i>Lampedusa</i> ( <i>Lampedusa</i> ) <i>lopadusae</i>	<i>Lampedusa</i> ( <i>Lampedusa</i> ) <i>lopadusae</i>	<i>Lampedusa</i> ( <i>Lampedusa</i> ) <i>lopadusae</i>	<i>Lampedusa</i> <i>lopadusae</i>
<i>Clausilia imitatrix</i> O. Boettger, 1879	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>imitatrix</i>	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>imitatrix imitatrix</i>	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>imitatrix</i>	<i>Lampedusa</i> <i>imitatrix imitatrix</i>
<i>Clausilia (Papillifera) melitensis</i> Caruana-Gatto, 1892	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>melitensis</i>	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>imitatrix melitensis</i>		<i>Lampedusa</i> <i>imitatrix melitensis</i>
<i>Lampedusa (Imitatrix) Gattoi</i> Soós, 1933	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>Gattoi</i>	<i>Lampedusa</i> ( <i>Imitatrix</i> ) <i>imitatrix gattoi</i>		<i>Lampedusa</i> <i>imitatrix gattoi</i>
<i>Clausilia syracusana</i> Philippi, 1836	<i>Lampedusa</i> ( <i>Muticaria</i> ) <i>syracusana</i>	<i>Muticaria</i> <i>syracusana syracusana</i>	<i>Muticaria</i> <i>syracusana</i>	<i>Lampedusa</i> <i>syracusana syracusana</i>
<i>Clausilia oscitans</i> Charpentier, 1852	<i>Lampedusa</i> ( <i>Muticaria</i> ) <i>syracusana</i> var. <i>oscitans</i>	<i>Muticaria</i> <i>syracusana oscitans</i>	<i>Muticaria</i> <i>scalaris oscitans</i>	<i>Lampedusa</i> <i>syracusana oscitans</i>
<i>Clausilia scalaris</i> L. Pfeiffer, 1848	<i>Lampedusa</i> ( <i>Muticaria</i> ) <i>scalaris</i>	<i>Muticaria</i> <i>syracusana scalaris</i>	<i>Muticaria</i> <i>scalaris scalaris</i>	<i>Lampedusa</i> <i>syracusana scalaris</i>
<i>Clausilia Mamotica</i> Gulia, 1861	<i>Lampedusa</i> ( <i>Muticaria</i> ) <i>Mamotica</i>	<i>Muticaria</i> <i>syracusana mamotica</i>		<i>Lampedusa</i> <i>syracusana mamotica</i>

HOLYOAK: MALTESE CLAUSILIIDAE



PLATE 21

shells of Maltese Clausiliidae.

A, B *imitatrix* (cliff edge at limits of tal Merhia); C, D *melitensis* (Rdum il Madliena); E, F *gattoi* (islet of Filla); G *imitatrix* × *syracusana* (?) (uppermost reaches of Santi valley); H *imitatrix* × *oscitans* (tal Merhia); all specimens were collected by Martin Thake on Malta between 1975 and 1984; all are in Colln. D. T. Holyoak & M. B. Seddon.

Scale marked at intervals of 1.0 mm.





PLATE 22

shells of Maltese Clausiliidae.

A *syracusana* (Ghajn Tuffieha, Malta); B, C *syracusana* × *oscitans* (B Naghag il Bahar, Gozo; C Borg in Nadur, Malta); D *oscitans* (tal Merhia, Malta); E *syracusana* × *scalaris* (Mistra, Malta); F *scalaris* (Mistra, Malta); G *mamotica* (Munxar, Gozo); H *melitensis* × *oscitans* (SSE. of Dingli, Malta); all specimens were collected by Martin Thake in the Maltese Islands in 1983; all are in Colln. D. T. Holyoak & M. B. Seddon. Scale marked at intervals of 1.0 mm.



Synonym: *Clausilia filfolensis* Caruana-Gatto, (unpublished);

Range: islet of Filfla (off south-western Malta).

**Lampedusa syracusana** (Philippi, 1836)

**L. s. syracusana**

Based on: *Clausilia syracusana* Philippi, 1836;

Synonyms: *Clausilia macrostoma* Cantraine, 1841; *Clausilia oscitans* var. *pseudosyracusana* Caruana-Gatto, 1892 (Zilch (1977) regarded this as a synonym of *oscitans* but his figure of a syntype (*op. cit.*, T. 9, fig. 38) shows the coarser ribbing of *syracusana*); *Clausilia syracusana* var. *scabrida* Monterosato, 1893;

Range: southern Sicily (near Syracuse); Maltese Islands (Malta, Gozo, Comino, Cominotto, St. Paul's Island).

**L. s. oscitans** (Charpentier, 1852)

Based on: *Clausilia oscitans* Charpentier, 1852;

Synonyms: *Clausilia oscitans* Férussac, 1822 (*nomen nudum*); *Isabellaria intrusa* O. Boettger, 1877; *Clausilia syracusana* (part) Feilden, 1879; *Papillifera* (*Isabellaria*) *oscitans* A. J. Wagner, 1919;

Range: Malta and Gozo.

**L. s. scalaris** (L. Pfeiffer, 1848)

Based on: *Clausilia scalaris* L. Pfeiffer, 1848;

Synonym: *Clausilia Delicatae* Gulia, 1861;

Range: Malta (local: St. Paul's Bay).

**L. s. mamotica** (Gulia, 1861)

Based on: *Clausilia Mamotica* Gulia, 1861;

Range: Gozo (local: near Munxar).

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# BARBIERELLA (BIVALVIA:LUCINACEA) A TETHYAN RELICT SPECIES LIVING IN THE RED SEA

P. G. OLIVER<sup>1</sup> AND M. ABOU-ZEID<sup>2</sup>

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*Abstract:* The genus *Barbierella* is redefined and a new species is described. *B. scitula* n.sp. extends the stratigraphic and geographic ranges of the genus from the Eocene–Miocene of Europe to the Recent of the Red Sea. This suggests that *Barbierella* is of tethyan origin and that *B. scitula* is a relict of a once much more widespread genus.

## INTRODUCTION

Collections of molluscs from the Gulf of Suez were recently received from the Oil Pollution Research Unit, Orielton. The use of grab sampling resulted in the presence of numerous smaller species amongst which were examples of an unusually sculptured lucinid bivalve.

Initial attempts at identification were unsuccessful until we examined plates of Eocene molluscs in Cossmann (1905) where we noted a strong similarity to *Phacoides* (*Here*) *naviculus* Cossmann. This species had been referred to *Barbierella* by Chavan (1938) but the lack of figures in that paper and the scant description of the genus in Chavan (1969) led us to overlook this genus. Chavan (1938, 1969) states that the sculpture is cancellate and that the hinge is weak but these statements were found to be misleading. Consequently this paper, which is part of a revision of the Red Sea Bivalvia, redefines the genus *Barbierella* and describes the recent Red Sea form as new.

## BARBIERELLA CHAVAN, 1938

*Type species:* *Lucina barbieri* Deshayes, 1858; Eocene – Paris Basin

*Definition:* Shell small, less than 10 mm, ovate-trigonal with a prominent posterior sulcus which gives rise to a posterior marginal truncation. Umbos inturned, prosogyre, lunule deeply excavated. Sculpture of scalloped concentric lamellae with an underlying series of radial undulations. Hinge teeth reduced; in the right valve is a single prominent cardinal with single anterior and posterior laterals which are reduced or absent; in the left is a prominent cardinal socket bounded by two ‘cardinal’ teeth which are no more than extensions of the edges of the lunule and ligament fossa, lateral teeth are greatly reduced or wanting. Ligament wholly external. Inner margin undulating. Anterior adductor scar short, divergent from the pallial line.

*Range:* Eocene—Recent, Europe—Red Sea

*Species included:* *B. barbieri* Deshayes; Eocene—Paris Basin

*B. naviculus* Cossmann; Eocene—Loire

*B. miobarbieri* Sacco; Miocene—Italy

*B. scitula* n.sp.; Recent—Red Sea

<sup>1</sup> Dept. of Zoology, National Museum of Wales, Cardiff CF1 3NP, Wales, U.K.

<sup>2</sup> Al-Azhar University, Cairo. Present address: Dept. of Zoology, National Museum of Wales, Cardiff CF1 3NP, Wales, U.K.



*Remarks:* Chavan (1938, 1969) describes the sculpture as 'cancellate' but this is not accurate as in both the genotype and *B. scitula* the sculpture is predominantly of concentric lamellae. The scalloped form of these lamellae give a pseudocancellate appearance but there are no radial ribs actually intersecting the lamellae. Chavan also describes the teeth as weak but this is not accurate as the single right valve cardinal and left valve socket form a very strong hinge. Admittedly the lateral teeth are obsolete although not consistently so as evidenced by the single anterior right valve lateral in *B. barbieri*.

Chavan (1938) stated that *Barbierella* was most closely related to *Cavilucina* but there are also strong resemblances to *Recurvella*. Chavan's (1938, 1969) reliance on hinge formulae seems doubtful given that there is considerable variation in the expression of the lateral teeth. Bretsky's (1976) arrangement seems much more acceptable and it is unfortunate that she restricted her review to the North American fauna which does not contain examples of *Barbierella* or *Cavilucina*.

The stratigraphic range of *Barbierella* was given by Chavan (1969) as Eocene to Recent and the geographic range as Europe–Indian Ocean. This contrasts with his 1938 paper where there was no mention of Recent forms and where he stated that *Here inopinata* Cossmann from India belonged to *Recurvella*. We have carried out a complete literature search and have been unable to locate any reference of a Recent species or figures of any lucinid which could be referred to *Barbierella*. The occurrence of *Barbierella* in the Eocene – Miocene of Europe and now in the Recent of the Red Sea suggests a biogeographic link between the two. Given the Eocene origin of *Barbierella* this link would appear to be Tethyan.

***Barbierella scitula* n. sp.** (Pl. 23, figs. 1–4)

*Holotype:* NMW.Z.<sup>3</sup>1982.68.1; Off Ras Budran, Gulf of Suez, Red Sea, 30 metres, sand.

*Paratype:* BM(NH) 186030: As holotype

*Paratype:* NMW.Z.1986.11.1; Zeit Bay, Gulf of Suez, Red Sea.

*Dimensions*

	Length (mm)	Height (mm)	Tumidity
Holotype	8.24	7.36	4.24
Paratype [BM(NH)]	8.70	7.65	5.18
Paratype [NMW]	9.43	8.65	5.42

*Shell:* Equivalve, ovate-trigonal, slightly inequilateral umbos just behind the midline, posterior margin truncate indented, posterior sulcus very deep, lunule deeply concave. Sculpture of 27–32 recurved scalloped concentric lamellae but of these 15–17 are small and restricted to the post umbonal area and the remaining 12–15 lamellae are very prominent and widely spaced. Along the margins of the posterior sulcus the scalloping is developed into prominent spines. The underlying radial undulations are most evident as 2–3 anterior troughs. Hinge with 1 strong cardinal tooth in the right valve and a deep cardinal socket in the left valve. Lateral teeth obsolete. The ventral edges of the lunule interlock that of the left valve fitting into the right valve. Ligament external. Internal margin deeply fluted forming a strong interlocking series of ridges and depressions. The ventral one third of the anterior adductor scar diverges from the pallial line.

*Colour:* White.

<sup>3</sup>*Institutional abbreviations*

BM(NH) British Museum (Natural History)  
 MHNP Museum d'Histoire Naturelle de Paris  
 NMW National Museum of Wales

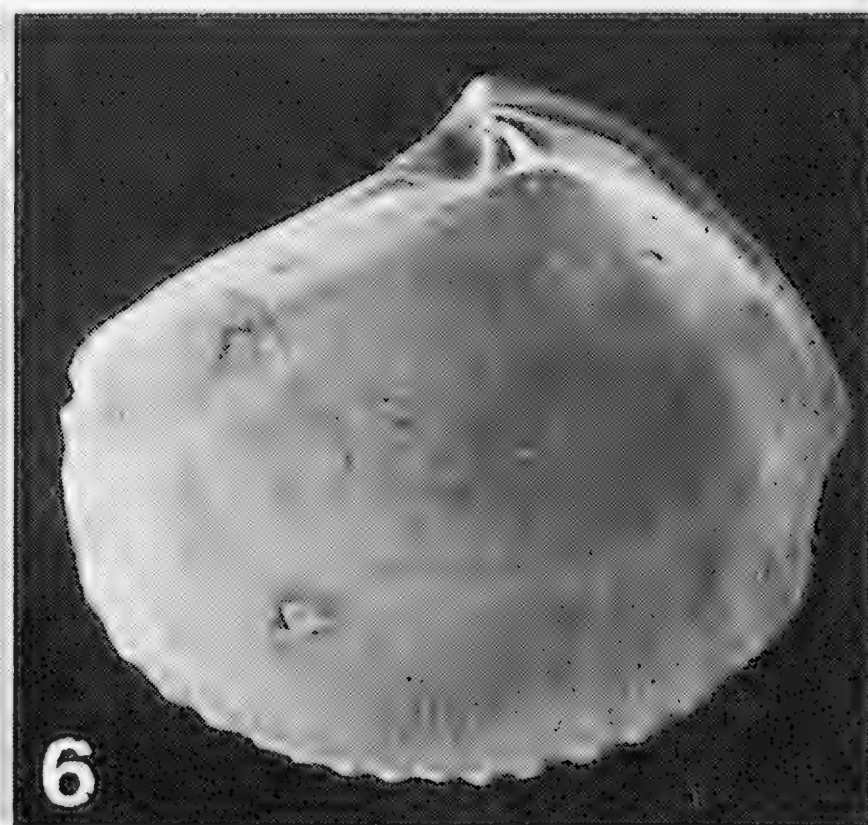
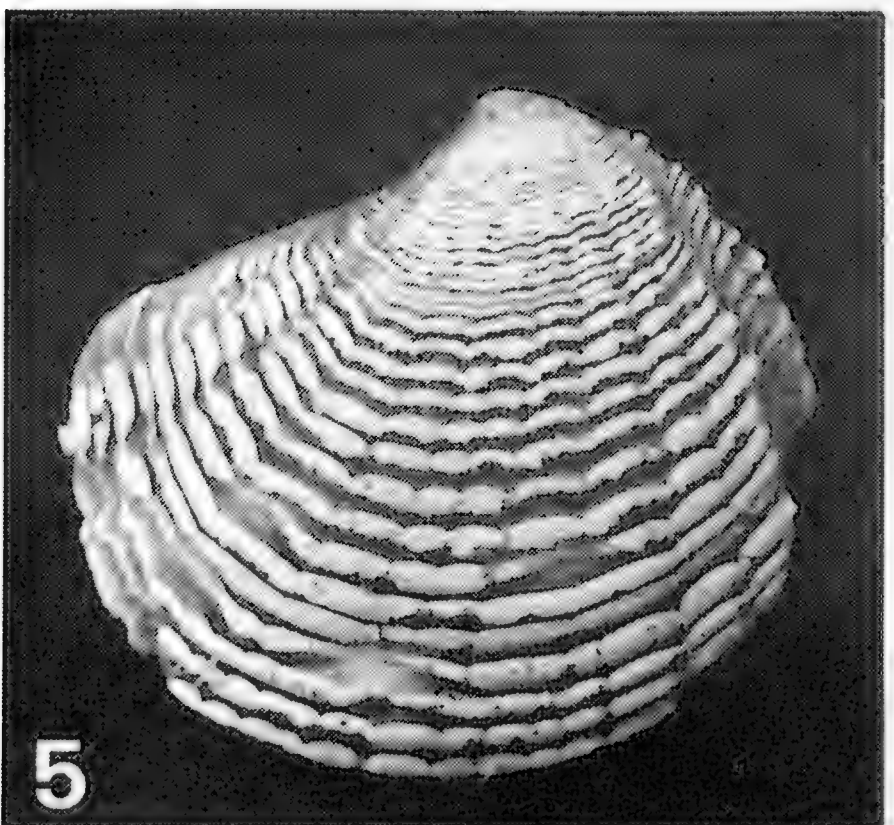
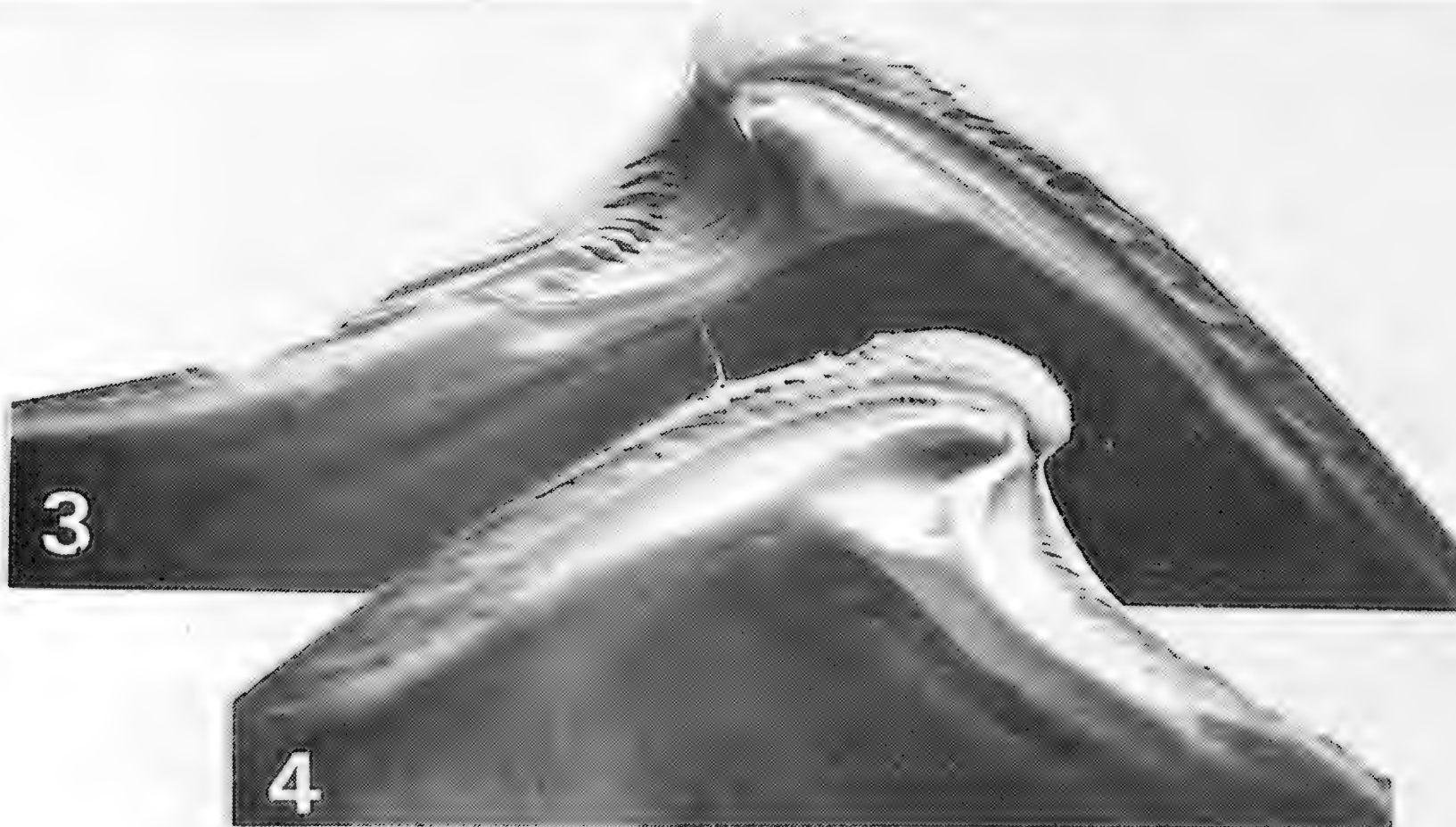
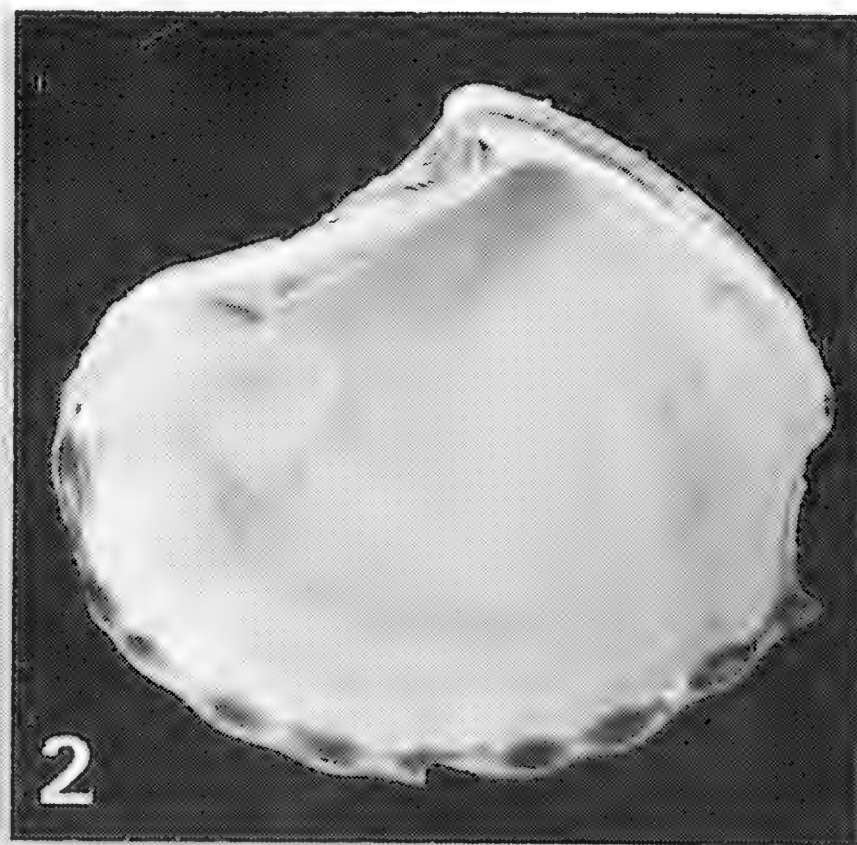
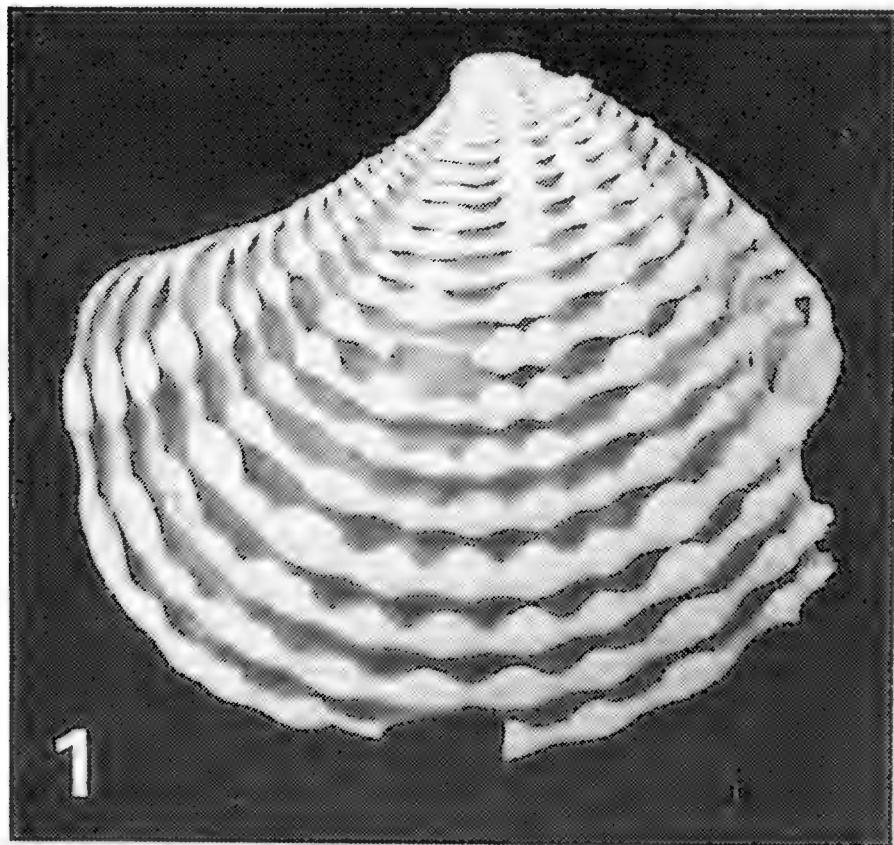


PLATE 23

Figs. 1, 2 *Barbierella scitula* n.sp. Holotype NMW.Z.1982.68.1. Actual length 8.24 mm.

Figs. 3, 4 *Barbierella scitula* n.sp. Holotype. Scanning Electron Micrographs of the hinge (3) Right Valve, (4) Left Valve.

Figs. 5, 6 *Barbierella barbieri* Deshayes. MHNP-Pal. B53507. Actual length (5) 7.14 mm, (6) 7.62 mm.





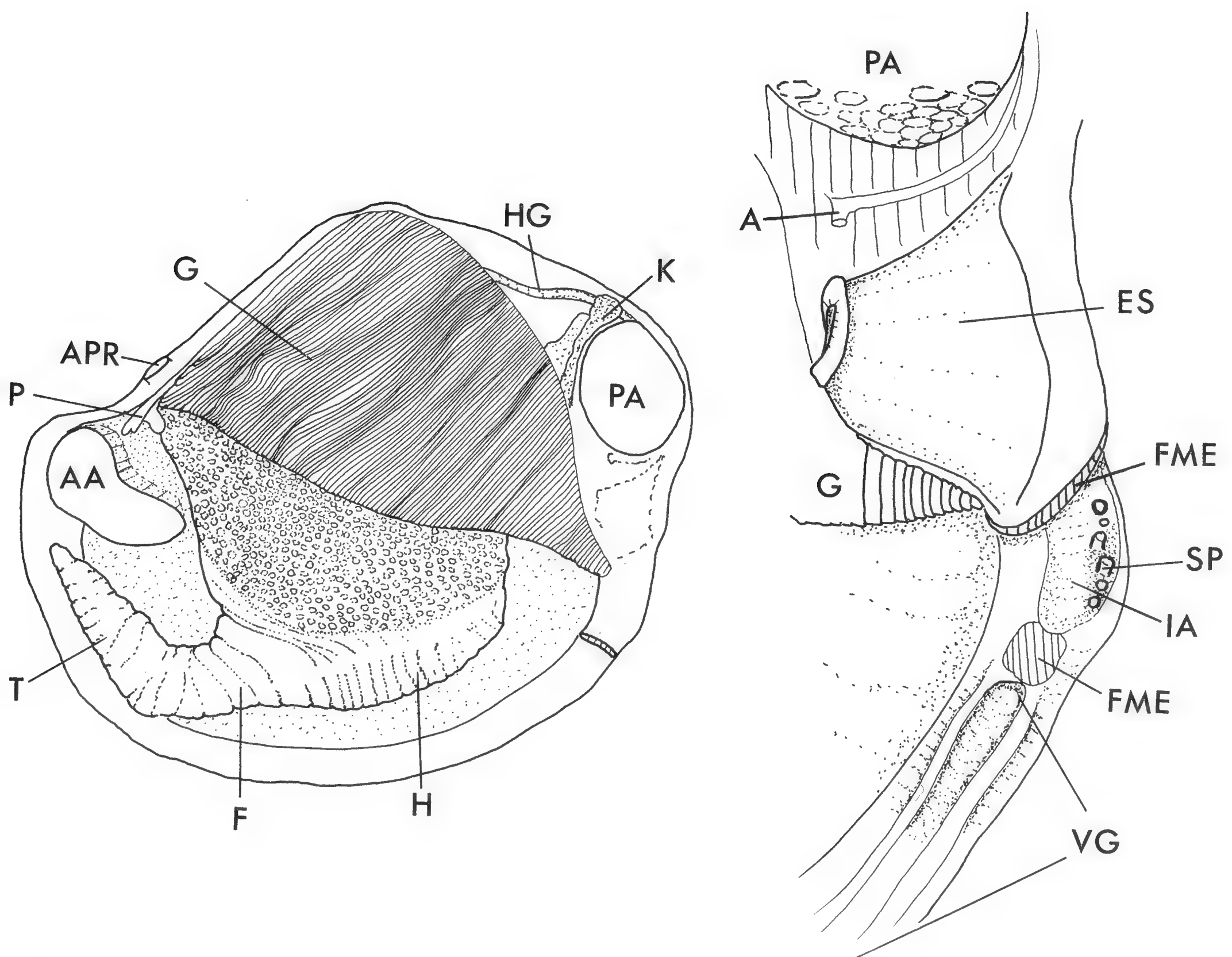


Fig. 1 Anatomy of *Barbieriella scitula* viewed from the left side with the mantle removed.

Fig. 2 Detail of the posterior mantle edge of *Barbieriella scitula*.

#### *Abbreviations used in text figures*

A anus, AA anterior adductor muscle, APR anterior pedal retractor, ES siphon, F foot, FME fused mantle edge, G gill, H heel, HG hind gut, IA inhalent aperture, K kidney, P palps, PA posterior adductor muscle, SP sensory papillae, T toe, VG ventral gape

*Anatomy:* (Figs. 1, 2) Gills of single demibranchs. Palps small with no apparent ridges. Mantle margins unfused except posteriorly where there is an exhalent siphon and a small inhalent aperture. The latter is bordered on either side by six sensory papillae. No mantle gills are present. The foot is vermiform, the heel is elongate and not well demarcated from the toe.

*Derivatio nominis:* *scitula* L.:—elegant.

*Remarks:* The sculpture, posterior sulcus and hinge are typical of the genus *Barbierella* as evidenced by comparison with the genotype *B. barbieri* (Pl. 23, figs. 5, 6). *B. scitula* differs in that the sculpture is more coarse, the anterior lateral teeth are obsolete and the marginal

interlocking crenulations are much stronger. These differences apply to the other Neogene species.

In comparison to other Indo-Pacific Lucininae there is little cause for confusion as the sculpture of *Barbierella* is very distinctive. In the Red Sea the only other species with prominent concentric lamellae is *Lucina dentifera* but in that species the lamellae are more numerous, not recurved or scalloped, the hinge possesses lateral teeth and the lunule is not excavated.

#### ACKNOWLEDGEMENTS

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# A RECLASSIFICATION OF THE RECENT GENERA OF THE SUBCLASS PROTOBRANCHIA (MOLLUSCA:BIVALVIA)

J. A. ALLEN<sup>1</sup> AND FIONA J. HANNAH<sup>1</sup>

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## INTRODUCTION

From the earliest writings to the present, malacologists have experienced great difficulty in separating clearly and defining adequately the protobranch taxa (eg. Seguenza 1877, Jeffreys 1881, Dall 1886, Verrill & Bush 1897, 1898, Iredale 1929, Theile 1935, Schenck 1934, 1939, Ockelmann 1954, Dell 1955, 1964, McAlaster 1964, Newell 1969, Knudsen 1970, Sanders & Allen, 1973). The difficulties are due in great part to the conservativeness of the form of the protobranch shell, but also to the lack of adequate description and poor knowledge of the anatomy.

Although species from circumscribed geographical areas can be more or less easily separated, when the world wide array of species is reviewed subtle gradations of morphology, both internal and external, become apparent and make clear cut classificatory divisions extremely difficult to establish. The gradation can be observed at all levels below Order, thus families, as well as genera and species are difficult to define.

The Protobranchia have one of the longest recorded evolutionary histories within the Animal Kingdom and date back to the Cambrian (Allen 1985). The array of shell forms already fully established in the Ordovician is little different in extent and composition to that which is present in the Recent. Presumably this is in part a result of a reproductive design that results in a very slow gene flow which is in turn accentuated by an inherent slow mutation rate. The consequence of this, particularly manifest in the deep sea protobranch fauna (an environment in which the Subclass dominates not only the Mollusca, but also much of the invertebrate fauna), is that although amazingly conservative in form, subtle differences in shape are such that great difficulty can be experienced not only in delimiting specific, subspecific and population variations but also in establishing generic and familial distinctions in the broad continuum of forms. Paradoxically, this situation makes it essential that divisions are clearly established, not only to bring order to the Subclass but to identify and define the main evolutionary trends.

This problem has been acknowledged by past workers on the group, but it is no more succinctly and elegantly set out than by Verrill & Bush (1897) nearly a century ago in the first real attempt to define the taxa of the Subclass. Since then most experts have been deterred by the difficulties and size of the problem, they have avoided the global complexities and followed their own 'parochial whim' either neglecting to improve the poor definitions of earlier workers or, as in the case of Iredale (1929), confusing the issue further by adding genera with little or no definition or even consideration of those that already exist. The result is a confusing array of regional usages that are not collated.

<sup>1</sup> University Marine Biological Station, Millport, Isle of Cumbrae, Scotland.



Because of recent and on going studies of the deep sea protobranch fauna (see Allen 1978), with dramatically increased numbers of new species described and many others in the process of description, although far from easy there is an even more urgent need to establish clear definitions. We have endeavoured to work within existing names and definitions. Here we name and define to the subgeneric level and give the cited reference source in the bibliography not only to the recognized name but also to the accepted synonyms. We also list other names that have been established in the literature which we believe are synonyms and presently superfluous but, in doing so, recognise that future workers might wish to define subdivisions and variations on what we propose here and may need to use them. We do not include misspelt names recorded as erroneous by Vokes (1967) nor do we list type species in the text, however, these can be traced via the bibliography. Thus, there is access to earlier recorded definitions and, we would hope, there will be less need to erect new names.

## SYNOPSIS OF CLASSIFICATION

*Class* **Bivalvia***Subclass* *Protobranchia*

## Order Solemyoida

Family Solemyidae<sup>1</sup>Family Nucinellidae<sup>1</sup>

## Order Nuculoida

## Superfamily Nuculacea

Family Pristiglomidae

Family Nuculidae

## Superfamily Nuculanacea

Family Tindariidae

Family Saturniidae

Family Lametilidae

Family Nuculanidae

Subfamily Ledellinae

Subfamily Spinulinae

Subfamily Nuculaninae

Family Yoldiidae

Subfamily Yoldiinae

Subfamily Yoldiellinae

Family Siliculidae

Family Malletiidae

<sup>1</sup> Earlier classifications of the Protobranchia have included the Superfamily Solemyacea Gray 1840. That we have not done here is to avoid repetition. If included the Superfamily would embrace only one family (Solemyidae) with the same definition. Furthermore, it would then be necessary to erect a second Superfamily (Nucinellacea) also embracing one family (Nucinellidae) with the same definition.

## CLASS BIVALVIA LINNÉ, 1758

*SUBCLASS* *PROTOBRANCHIA* PELSENEER, 1889

Bivalvia with foot sagittally and longitudinally grooved, sole margins papillate, fringed; gill

filaments usually, plate-like, unreflected with abfrontal cilia; byssus gland absent. (A so-called pedal or 'byssal' gland in heel of foot is often present. This does not produce a byssus and has a structure totally different from that of the lamellibranch byssus gland).

*Order* **Solemyoida** Dall, 1889

Equivalve shell; hinge teeth if present not chevron-shaped; periostracum thick; ligament usually external, short, thick, opisthodetic; gill well developed, broad, covering body; palps minute, triangular, close to mouth.

*Family* **Solemyidae** Gray, 1840

Shell, elongate, gaping, posterior and anterior margins rounded, weakly calcified particularly at ventral margin; hinge teeth absent; extensive ventral mantle fusion; lumen of hind gut extremely narrow or wanting.

Genus **Solemya** Lamarck, 1818

[=*Solenomya* Children, 1823, *Stephanopus* Scacchi, 1833]

Shell elongate, oval or subrectangular, compressed or circular in transverse section, gaping anteriorly and posteriorly, umbos level with dorsal margin; external part of ligament within a deep groove between shell margin and oblique chondrophore, opisthodetic, either entirely posterior to umbo or with slight extension anterior to umbo; periostracum thick, glossy, extending beyond ventral shell margin; moderately heteromyarian, posterior adductor muscle smaller than anterior; stomach with dorsal hood.

Subgenus **Solemya** s.s. (Fig. 1)

Ligament posterior to umbos, extended by thin strip that descends internally within the valves anterior to chondrophore; chondrophore without buttress or ridges.

Subgenus **Petrasma** Dall, 1908 (Fig. 2)

Ligament wholly posterior to umbo; chondrophore with 1 or 2 internal ridges.

Subgenus **Solemyarina** Iredale, 1931 (Fig. 3)

[=*Zesolemya* Iredale, 1939]

Greater portion of ligament between chondrophore and dorsal margin, but with small extension anterior to chondrophore, partly at shell margin and partly and narrowly internal to it; an internal ridge diverges at an acute angle from chondrophore skirting dorsal margin of posterior adductor.

Genus **Acharax** Dall, 1908 (Fig. 4)

Shell elongate, oval or subrectangular, compressed or circular in transverse section; ligament wholly external, opisthodetic, supported by nymphs; without chondrophore.

*Family* **Nucinellidae** Vokes, 1956

Shell equivalve, triangular or nukuloid, well calcified; hinge teeth present and comprise series of cardinals and elongate laterals; buttress skirts dorsal margin of anterior adductor muscle; ligament large, at margin of hinge plate, predominantly external; monomyarian or extreme heteromyarian, anterior adductor very large; mantle not fused ventrally; stomach without dorsal hood; lumen of hind gut not markedly narrow.

Genus **Nucinella** Wood, 1851

[=*Pleurodon* Wood, 1840 (*non* Harlan, 1831), *Nuculina*, 1829 d'Orbigny 1844 (*non* Porro, 1837), *Cyrellona* Iredale, 1929, *Neopleurodon* Hertlein & Strong, 1940]

Description as for family.

Subgenus **Nucinella** s.s. (Fig. 5)

Shell nuculoid; cardinal teeth arrayed in series anterior and posterior to umbo, the division between the series may be indistinct; ligament inserted in part externally and in part on dorsal margin of hinge plate.

Subgenus **Huxleyia** A. Adams, 1860 (Fig. 6)

[=*Cyrella* A. Adams, 1860, *Diabolica* Jousseaume, 1897, *Cyrellista* Iredale, 1929]

Shell markedly inequilateral, wedge-shaped, hardly developed anterior to umbos, surface with concentric striae; cardinal teeth in single series posterior to umbo; ligament inserted on dorsal margin of hinge plate in rounded fossette.

### Order **Nuculoida** Dall, 1889

Shell equivalve; periostracum well developed but not exceptionally thick; taxodont hinge teeth; gills posterior, not large, cover only small part of body; palps large, extending antero-laterally over body, with palp proboscides.

### Superfamily **Nuculacea** Gray, 1824

Shell round or triangular; ligament usually internal; no mantle fusion, siphons absent, without posterior mantle tentacle and feeding aperture, inhalent current antero-ventral; mouth adjacent to posterior dorsal limit of adductor muscle; gill axis oblique to horizontal plane, gill plates opposite; palps large, broad and deep; foot relatively square in lateral view, neck broad; hypobranchial glands present; without anterior mantle sense organ.

Family **Pristiglomidae** Sanders & Allen, 1973

Shell round; gills small, with markedly reduced number of short filaments; hind gut looped or coiled about both sides of the stomach.

Genus **Pristigloma** Dall, 1900 (Fig. 7)

[=*Glomus* Jeffreys, 1876]

Shell fragile, smooth or with faint concentric striae; hinge teeth lamellar or chevron-shaped, anterior teeth few in number or absent, when present situated close to umbo; umbos raised and posteriorly directed; ligament internal, opisthodetic, long and narrow; hind gut with several loops.

Genus **Microgloma** Sanders & Allen, 1973 (Fig. 8)

Shell minute, broadly oval, relatively robust with concentric ridges; equal or approximately equal small number of chevron teeth on either side of umbo; umbos posterior to mid line moderately low in profile, medially directed; ligament internal, amphidetic, relatively broad; adductor muscles relatively moderate in size, equal or nearly so; hind gut coiled.



Genus **Pseudoglomus** Dall, 1898 (Fig. 9)

Shell minute, round, fragile, smooth or very fine concentric sculpture; umbo central; chevron teeth, few, anterior and posterior series equal or approximately equal in number, little or no gap between series, extend to level of inner margin of adductor muscles; ligament amphidetic, short, barely internal, visible externally at base of small umbonal pit; adductor muscles relatively large, equal in size.

Family **Nuculidae** Gray, 1824

Shell ovate or triangular, posteriorly truncate; umbos posteriorly directed; gills moderately large with relatively large number of elongate plates; hind gut on right side of body, numerous non-aligned coils.

Genus **Nucula** Lamarck, 1799

[=*Lembulus* Leach in Sowerby, 1842 (*non Lembulus* Risso, 1826)]

Shell ovate or triangular, smooth or with concentric sculpture, with or without fine riblets on lunule and escutcheon, outer layer of shell formed with or without radial elements, margin crenulate or not crenulate, periostracum dull or polished; ligament internal, relatively short, oblique or perpendicular to hinge plate.

Subgenus **Nucula** s.s. (Fig. 10)

[=*Lamellinucula* Schenck, 1944]

Shell ovate or triangular, stout, smooth or concentric sculpture, margin crenulate, usually radial elements; hinge plate angulate, proximal teeth close to relatively small chondrophore; ligament oblique.

Subgenus **Pronucula** Hedley, 1902 (Fig. 11)

Shell ovate or triangular, margin crenulate, variable radial sculpture; hinge plate arched, hinge teeth not continuous below umbo, proximal teeth distant from ventrally projecting chondrophore; ligament perpendicular.

Subgenus **Brevinucula** Thiele, 1934 (Fig. 12)

Shell relatively small, short, deeply triangular, robust with high lustre, radial elements not obvious; hinge very strong, not angulate, resilium not developed into chondrophore; ligament perpendicular.

Genus **Nuculoma** Cossmann, 1907 (Fig. 13)

[=*Nuculopsis* Woodring 1925 (*non* Girty 1911), *Leionucula* Quenstedt 1930, *Ennucula* Iredale 1931, *Austronucula* Powell 1939]

Shell elongate-ovate, moderately robust, outer layer of shell smooth, glossy, without radial elements, margin not crenulate; chondrophore may be present; ligament internal, small, oblique to hinge plate and may extend under anterior proximal teeth.

Genus **Acila** Adams & Adams, 1858

Shell, ovate triangular, robust, divaricate sculpture, ventral margin strongly crenulate; ligament internal, oblique.

Subgenus **Acila** s.s. (Fig. 14)

Shell postero-ventrally slightly rostrate, postero-ventral margin slightly sinuate.

Subgenus **Truncacila** Grant & Gale, 1931 (ex Schenck ms) (Fig. 15)

Shell relatively truncate, without rostrum, postero-ventral margin not sinuate.

*Superfamily* **Nuculanacea** Gray, 1824

Shell usually posteriorly elongate, occasionally equilateral, very occasionally anteriorly elongate; mantle may be fused and extended posteriorly to form a siphon or siphons, or may be papillate; posterior tentacle usually present, anterior mantle sense organ present; inhalent current posterior; mouth at varying distance from adductor muscle; gill axis parallel to horizontal plane or nearly so; palps elongate; foot elongate with narrow neck; ligament internal and/or external.

*Family* **Tindariidae** Sanders & Allen, 1977

Shell ovate, robust, concentric sculpture, occasionally with radial lines; hinge plate strong with well developed chevron teeth continuous below umbo; umbos large, medially or anteriorly directed; ligament external, more elongate posteriorly than anteriorly; true siphons lacking, posterior inhalent aperture fringed with elongate papillae; palps relatively small, with few ridges; hind gut, single loop to right of body which may penetrate mantle.

Genus **Tindaria** Bellardi 1875, (Fig. 16)

[=*Deminucula* Iredale 1931]

Description as for family.

*Family* **Saturniidae** (*new family*)

Shell usually robust and inflated, moderately large, not particularly elongate, more or less ovate, may be slightly rostrate or postero-ventrally angulate, usually marked concentric sculpture; hinge teeth taxodont, continuous or interrupted below umbo; ligament external and/or internal; siphons present; hind gut either a single loop to right of body or a complex series of loops and coils to left and right of body.

Genus **Saturnia** Dall, 1881 (Fig. 17)

[=*Neilonella* Seguenza, 1877, *Austrotindaria* Fleming, 1948]

Shell moderately robust, relatively wide, strong concentric sculpture, anterior margin rounded, posterior margin slightly attenuate and may be moderately angular, without rostrum or carina; hinge plate moderately strong, many chevron teeth, small gap between anterior and posterior series; ligament opisthodetic, largely external with very small, internal resilifer; siphonal embayment shallow; hind gut single loop to right of body.

Genus **Pseudotindaria** Sanders & Allen, 1977 (Fig. 18)

Shell robust, relatively wide, anteriorly and posteriorly rounded, not carinate, strong concentric sculpture; hinge plate strong with numerous chevron teeth continuous below umbo; ligament external, anterior part short, posterior part elongate; hind gut with complex series of loops and coils to right and left of the body.

Genus **Neilo** Adams, 1854 (Fig. 19)

[=*Carinineilo* Kuroda & Habe, 1971]

Shell robust, relatively wide, moderately elongate and posteriorly extended, postero-dorsal margin straight or slightly concave, carinate, posteriorly truncate or slightly rostrate,

postero-ventral margin maybe somewhat sinuous, two rounded radial ridges from umbo to posterior margin; hinge plate, well developed; numerous chevron teeth, anterior and posterior series separate and may differ in size (anterior larger); ligament external; siphons long.

Genus **Protonucula** Cotton, 1930 (Fig. 20)

Shell fragile, oval, compressed, glossy, concentric sculpture; hinge plate narrow, chevron teeth, squat and broad, continuous below umbo, no chondrophore; umbo prominent; ligament not known, but from marginal resilifer probably small, external, amphidetic.

Family **Lametilidae** Allen & Sanders, 1973

Shell moderately strong, ovate, tumid, umbo low, relatively elongate, without lunule and escutcheon; hinge weak, 2–4 elongate lamelliform teeth either anterior or posterior to umbo, chevron-shaped teeth may or may not be present; ligament amphidetic, internal; siphons present, ventral margin of inhalent siphon not fused; gill plates broad, leaf-like; hind gut with loops to right and left side of body that pass across dorsally and ventrally posterior to stomach and ventrally anterior to stomach; foot relatively square in outline, well defined neck.

Genus **Lametila** Allen & Sanders, 1973 (Fig. 21)

Shell smooth, somewhat inequilateral, rounded anteriorly and posteriorly; hinge teeth lamelliform, two on each side, weak; hind gut with two loops on right of body; adductor muscles approximately equal in size.

Genus **Prelametila** Allen & Sanders, 1973 (Fig. 22)

Shell smooth, somewhat inequilateral, rounded anteriorly and posteriorly; lamelliform and taxodont teeth present; hind gut with four loops on right of body; anterior adductor muscle larger than posterior.

Genus **Phaseolus** Monterosato, 1875 (Jeffreys ms) (Fig. 23)

[=*Silicula* Jeffreys, 1879]

Shell very small, oval, equilateral or almost so, rounded anteriorly, slightly angulate posteriorly, transparent, glossy; 3–4 lamelliform hinge teeth on each side of umbo, form of gut as yet unknown.

Family **Nuculanidae** Adams & Adams, 1858

Shell elongate, may be moderately compressed, rostrate, if present gape restricted to short posterior margin where siphons protrude, usually with strong concentric sculpture; hinge teeth chevron-shaped; ligament internal or external with central internal part; siphons present.

Subfamily **Ledellinae** Allen & Sanders, 1982

Shell robust, moderately inflated, veneriform or ovate with short rostrum, posterior angulation or rostrum medial or submedial, concentric sculpture usually present, occasionally with radial striae; umbo approximately central; posterior dorsal margin convex, ventral margin maybe broadly flattened in older specimens, postero-ventral margin may be sinuous; hinge plate well developed; ligament internal and/or external; hind gut with various configurations; adductor muscles approximately equal in size, siphons usually combined to form single lumen, palps usually with relatively few ridges (<30).



Genus **Ledella** Verrill & Bush, 1897 (Fig. 24)

[=*Junonia* Seguenza, 1877 (*non* Hübner 1819), *Comitileda* Iredale, 1924, *Magaleda* Iredale, 1929]

Shell small, short, robust, surface matt, concentric sculpture, some species with superimposed indistinct radial lines; well-defined rostrum, usually unicarinate at margin of escutcheon; ventral margin may be broadly flattened, postero-ventral margin sinuous; anterior and posterior series of hinge teeth separated by ligament; amphidetic, mostly internal with very short, central outer layer visible externally; hind gut with three main types of configuration, single loop to right of body, coils to right of body, loops to left and right of body.

Genus **Tindariopsis** Verrill & Bush, 1897 (Fig. 25)

Shell veneriform, matt surface, short; rostrum indistinct, with slight radial ridge and furrow; posterior margin angulate; postero-ventral margin slightly sinuous; hinge teeth continuous below umbo; ligament short central internal part, elongate external part largely posterior to umbo, seated in notch at margin of hinge plate.

*Subfamily* **Spinulinae** Allen & Sanders, 1982

Shell moderately robust, laterally compressed, glossy surface, concentric sculpture; moderately elongate, supramedial rostrum; umbo approximately central; postero-ventral margin sinuous, postero-dorsal margin convex; ligament amphidetic with small central internal part, large external part; hind gut usually coiled on right of body, exceptionally a single loop to right of body; palps usually large with numerous ridges (>50).

Genus **Spinula** Dall, 1908

Description as for subfamily.

Subgenus **Spinula** s.s. (Fig. 26)

Shell with fine concentric sculpture, tip of rostrum a sharp point.

Subgenus **Bathyspinula** Filotova, 1958 (Fig. 27)

Shell with fine concentric sculpture with oblique intersecting striae, tip of rostrum blunt.

*Subfamily* **Nuculaninae** Allen & Sanders, 1982

Shell elongate, dorso-ventrally narrow, usually strong, well defined concentric sculpture, rostrum formed by extension of concave postero-dorsal margin; umbo anterior; postero-ventral margin if sinuous not deeply so; lumina of siphons usually entire; hind gut usually with single loop to right of body.

Genus **Nuculana** Link, 1807

[=*Leda* Schumacher, 1817, *Exocholeda* Iredale, 1939, *Kamaleda* Iredale, 1939, *Zygonoleda* Iredale, 1939, *Eptoleda* Iredale, 1939, *Thestyleda* Iredale, 1929, *Scaeoleda* Iredale, 1929, *Politoleda* Hertlein & Strong, 1940, *Costelloleda* Hertlein & Strong, 1940. *Robaia* Habe, 1958]

Shell robust, moderately and posteriorly elongate, postero-dorsally usually bicarinate fine or strong, concentric sculpture, escutcheon present, occasionally with radial ribs; hinge plate somewhat angular; ligament short, may be oblique, internal with small external part.

(This genus comprising of many species from the Continental Shelf epitomises the problems that ensue following description of the species from narrow geographical areas without reference to others elsewhere. World wide there is a continuum of form such that demarkation of subgroupings is not feasible despite clear distinction when the limits are

compared. Despite sympathetic understanding we can find no clear character(s) to distinguish the long list of genera synonymised here, however, it may be that some will prove of local use in identifying a 'form' within the continuum of species).

Subgenus **Nuculana** s.s (Fig. 28)

Shell moderately inflated, with fine to strong concentric sculpture, posterior ventral margin may be slightly sinuate, truncate rostrum, gaping where siphons protrude; umbo anterior.

Subgenus **Lembulus** Risso, 1826 (Fig. 29)

Shell relatively short, moderately inflated, bevelled oblique lines not coinciding with concentric sculpture, rostrum short, with radial ribs; ventral margin not sinuate, umbo anterior.

Subgenus **Jupiteria** Bellardi, 1875 (Fig. 30)

[=*Ledina* Sacco, 1898 (*non* Dall, 1898), *Sacella* Woodring, 1925, *Teretileda* Iredale, 1929, *Poroleda* Hutton, 1893 (in part)]

Shell relatively short, arcuate, subrostrate, not gaping posteriorly, moderately to strongly inflated, fine to strong concentric sculpture, transverse striations and short radial ridge may be present, carinate at margin of escutcheon, ventral shell margin not sinuate; umbo almost central; ligament small, internal, amphidetic, with posterior external part.

Subgenus **Costanuculana** Habe, 1951 (Fig. 31)

Shell moderately elongate, robust, compressed, conspicuous curved furrows on anterior and posterior parts of shell; radial margin of raised escutcheon indented from umbo to postero-ventral limit of moderate rostrum, ventral shell margin not sinuate; hinge teeth large, few in number; ligament strong.

Genus **Propeleda** Iredale, 1924 (Fig. 32)

[=*Poroleda* Hutton, 1893 (in part)]

Shell extremely elongate, thin, smooth, glossy, ill-defined concentric sculpture, 3/4 shell post-umbonal, not carinate, broadly rostrate, posteriorly truncate; umbo small; postero-dorsal margin barely concave, internal ridge from umbo along ventral margin of adductor to posterior margin, second ridge may be present from hinge plate to rostral margin; hinge plate moderately slender, anterior tooth series curves around adductor, posterior series extends posterior to adductor, proximal teeth lamellar (dorsal arm of chevron elongate, ventral arm lost or almost so); ligament opisthodetic, part external, part internal.

Genus **Adrana** Adams & Adams, 1858 (Fig. 33)

Shell extremely elongate, slender, lanceolate, relatively fragile, smooth, or with oblique sculpture, glossy; umbos almost central, barely raised; hinge plate with numerous small taxodont teeth, chondrophore large; ligament part internal, part external; siphons long, siphonal embayment deep.

Family **Yoldiidae** (*new family*)

Shell usually fragile, usually markedly compressed, ovate or elongate, usually extended posteriorly, may or may not be rostrate, may or may not gape, smooth or with fine concentric growth lines; postero-dorsal margin straight or convex, rarely concave; anterior and posterior hinge teeth series interrupted; ligament internal and/or external, may be carried on chondrophore; siphonate.

*Subfamily* **Yoldiinae** (*new subfamily*)

Shell moderately large, compressed, elongate, gapes slightly anteriorly and posteriorly, slightly rostrate, fine concentric sculpture occasionally with oblique or radial striae; ligament for most part internal; siphons fused ventrally, lumina entire.

Genus **Yoldia** Müller, 1842

[= *Tepidoleda* Iredale, 1939]

Shell fragile, compressed, elongate, tapering posteriorly, gaping slightly anteriorly and posteriorly, smooth or fine sculpture; poorly to moderately defined rostrum; postero-dorsal margin straight or slightly convex (except posterior limit may be somewhat upturned) with dorsal keel; hinge plate slender, chondrophore prominent; ligament largely internal, small external part extended by fused periostracum; siphons long, siphonal embayment deep.

Subgenus **Yoldia** s.s. (Fig. 34)

Shell elongate, at most very fine concentric sculpture, growth lines present; rostrum poorly defined, poorly defined posterior rostral ridge, with indication of posterior radial ridge; umbos mid dorsal, or slightly posterior; hinge teeth numerous, more anteriorly than posteriorly; chondrophore moderately large; ligament amphidetic.

Subgenus **Kalayoldia** Grant & Gale, 1930 (Fig. 35)

Shell elongate, concentric sculpture; rostrum narrowed, short, recurved; umbo posterior; ligament large, opisthodontic, internal part ovate attached to shallow pit, external part clearly visible; many more hinge teeth anteriorly than posteriorly; siphonal embayment deep.

Subgenus **Aeqviyoldia** Soot-Ryen, 1951 (Fig. 36)

Shell almost equilateral, concentric sculpture, fine anterior and posterior radial ridges and striae may be present, slightly rostrate; hinge teeth weak, few, anterior and posterior series equal in number or almost so; chondrophore broad.

Genus **Megayoldia** Verrill & Bush, 1897 (Fig. 37)

[= *Multidentata* Krishtofovitch, 1964]

Shell large, very broadly truncate, ill-defined ridge from umbo to posterior ventral margin, gaping posteriorly; rostrum poorly defined, posterior ventral marginal 'lobe', no escutcheon; large chondrophore; ligament partly internal, partly external, external part extended anteriorly and posteriorly in a narrow supramarginal furrow; siphonal embayment deep.

Genus **Cnesterium** Dall, 1898 (Fig. 38)

[= *Scissula* Dall, 1908]

Shell elongate, narrowed posteriorly, posterior oblique sculpture not coincidental with incremental lines, may be 3–4 anterior radial lines; rostrum recurved with dorsal margin keeled; hinge plate broad, with short chevron teeth; ligament partly internal and partly external, internal part moderately large, wedge-shaped between anterior and posterior hinge teeth series.

Genus **Orthoyoldia** Verrill & Bush, 1897 (Fig. 39)

Shell smooth, elongate, posteriorly slightly narrowed, rounded not rostrate, not carinate; hinge plate narrow, numerous chevron-shaped teeth; ligament very large, partly external, internally attached to deep, broad, chondrophore; siphonal embayment large and broad.



*Subfamily* **Yoldiellinae** (*new Subfamily*)

Shell small, usually compressed, ovate or elongate ovate, occasionally with ill-defined rostrum, not gaping, smooth, or very fine concentric sculpture; ligament amphidetic, largely internal; siphons of varied structure, siphonal embayment small; hind gut with various configurations.

Genus **Yoldiella** Verrill & Bush, 1897 (Fig. 40)

Shell small, fragile, usually fairly slender, subovate, usually glossy, no escutcheon or lunule, no carina, not gaping, occasionally fine concentric sculpture; sometimes postero-ventral margin very slightly sinuate, postero-dorsal margin slightly convex, may be posteriorly angulate; umbo usually anterior occasionally posterior or central; taxodont hinge teeth may or may not extend beyond inner limit of adductor muscles; no chondrophore; ligament amphidetic, but may extend somewhat posteriorly, large internal, small external component; hind gut with numerous configurations; mostly deep water species beyond shelf/slope break.

Genus **Portlandia** Mörch, 1857 (Fig. 41)

[=*Pseudoportlandia* Woodring, 1925, *Parayoldiella* Filotova, 1971]

Shell moderately small, slightly inflated, moderately fragile, oblong, posteriorly angular, more or less truncate, slightly rostrate, not gaping, escutcheon present, usually defined by weak or moderate carina, lunule may be present; usually glossy, smooth; postero-ventral margin may be sinuous, proximal postero-dorsal margin almost straight or slightly concave; umbo prominent, anterior; chondrophore variously developed; ligament amphidetic, largely internal with small part external; hind gut single loop to right of body; usually confined to continental shelf.

Genus **Adrenella** Verrill & Bush, 1898 (Fig. 42)

Shell small, oblong oval, compressed, very fine concentric sculpture, not rostrate; but posterior dorsal margin slightly upturned; hinge plate broad, relatively strong; shelf-like chondrophore present; ligament predominantly internal with small external part.

Genus **Microyoldia** Verrill & Bush, 1897 (Fig. 43)

Shell small, oblique or veneriform, compressed, no escutcheon; umbo anterior; hinge plate well developed, few anterior teeth, a few more posterior teeth with dorsal arm of chevron slightly extended; ligament relatively large, broadly triangular, internal part mostly posterior to umbo, external part barely visible.

Genus **Ovaleda** Iredale, 1925 (Fig. 44)

Shell fragile, glossy, deeply rounded, ovate, very faint rostration, raised escutcheon, very faint rostral ridge, faint concentric sculpture; postero-ventral margin not sinuous; umbo slightly anterior, moderately prominent; anterior and posterior hinge plates equal in length, occupy about 3/4 dorsal margin, triangulate chondrophore present; ligament amphidetic, largely internal.

Genus **Sarepta** A. Adams, 1860 (Fig. 45)

Shell fragile, nearly circular, compressed, sometimes fine concentric ridges, no escutcheon, no rostrum; posterior margin very slightly flattened; postero-ventral margin not sinuous; umbo central, small, but prominent; hinge plate very short approximately 1/2 dorsal margin, anterior and posterior taxodont teeth, equal in number, one arm of chevron extended; ligament amphidetic, obliquely triangular, largely internal, external part visible; hind gut with 3–4 loops to right and left of body.

*Family* **Siliculidae** Allen & Sanders, 1973

Shell elongate, extremely compressed, gaping, no escutcheon; umbo small, hardly seen above level of dorsal margin; hinge plate weak, teeth elongate, lamellar; ligament opisthodontic, internal, oblique; siphonate, ventral margin of inhalent siphon formed by adhesion and not fusion; outer gill plates half size of inner; mouth set far posterior to adductor muscle; hind gut single loop to right of body, or to right and left of body.

Genus **Silicula** Jeffreys, 1879 (Fig. 46)

Shell fragile, smooth, compressed; postero-dorsal margin straight or somewhat convex, posterior margin broadly truncate; lamellar teeth moderately long.

Genus **Lamellileda** Cotton, 1930 (Fig. 47)

Shell moderately strong, nuculanid in form, concentric sculpture, moderately compressed; postero-dorsal margin slightly concave, posterior margin sharply truncate; lamellar teeth long.

*Family* **Malletiidae** Adams & Adams, 1858

Shell smooth, moderately large, moderately inflated, oblong, not gaping, either not rostrate or slight indication of rostrum, no escutcheon, no carina; posterior margin blunt; ligament external, well developed; hind gut single loop on right side; siphons long, siphonal embayment well developed. (For a detailed analysis of the Family see Sanders & Allen 1985).

Genus **Malletia** Des Moulins, 1832 (Fig. 48)

[=*Solenella* Sowerby, 1832, *Ctenoconcha* Gray, 1840, *Pseudomalletia* Fischer, 1886, *Clencheria* Clarke, 1961, *Katadesmia* Dall, 1908]

Shell moderately large, moderately inflated, moderately fragile, without rostrum; posterior margin rounded; umbo anterior; hinge plate short with relatively few anterior teeth, anterior and posterior hinge teeth series separated; ligament opisthodontic.

Genus **Malletiella** Soot-Ryen, 1957 (Fig. 49)

[=*Bathymalletia* Kuroda & Habe, 1971].

Shell moderately large, ovate, moderately fragile, slightly rostrate, widely truncate; postero-ventral margin slightly sinuate; umbo anterior to midline; posterior and anterior hinge teeth continuous below umbo or almost so, ligament elongate, posteriorly set in groove at margin of hinge plate; siphonal embayment very short.

Genus **Minormalletia** Dall, 1908 (Fig. 50)

Shell small, fragile, inflated, smooth or fine concentric sculpture; umbo far anterior; ligament amphidetic.

EVOLUTION OF PROTOBRANCHIA

It is likely that the protobranchs were derived from an animal that had many of the characteristics of present day nucinellids. It would have had an ovate/triangular shell with a thick periostracum, the hinge would have been relatively stout with multiple cardinal teeth, possibly with a lateral tooth to each side. Whether the ligament was internal or external is debatable, but on balance we believe that it was probably predominantly external but not particularly elongate. The mantle margin would have been unfused, with

the inhalent flow anterior. The adductor muscles would have been equal in size, the gills protobranchiate and set obliquely across the mantle cavity, and the palps relatively small. The foot would have been large with a divided sole with a papillate margin. The gut probably was similar to that of *Nucinella*, with a relatively simple stomach, largely lined with a gastric shield. Sexes were separate. It must have led an active life moving through the upper layers of organically rich soft sediments.

From such a nucinellid form there was an array of radiating and sequential evolutionary steps. If success is to be measured in numbers of species and individuals then, the basic stock was not particularly successful. There are few nucinellids alive to-day and they differ relatively little from a basic hypothetical ancestor as described above. Their major evolutionary advance is the anterior enlargement of the mantle space, to accommodate the large, very active, antero-ventrally directed foot yet giving space for the intake of sedimentary material. This led to an unusual form of heteromyarianism in which the anterior adductor became very large and the posterior part of the mantle and shell became excessively truncate with the progressive loss of the posterior adductor muscle. The Solemyidae, while retaining much of the basic gill, palp and gut morphology of the nucinellids, took on a more sedentary mode of life but requiring an active well developed foot in order to form burrows. As an adaptation to a burrowing habit they took on an elongate cylindrical shape. Because of the reduced locomotary need and the supportive confines of the elongate 'Y'-shaped burrow, they no longer required a strong hinge mechanism. The ligament was relatively large and external. Similarly shell calcification diminished although not periostracal production, with the result that a flexible shell was produced that could form a cylinder, important in tube formation and tube dwelling.

The nukuloid morphology appeared very early in the evolutionary history of the protobranchs (no later than early Ordovician). Two major advances on the primitive form occurred, first the cardinal array of teeth extended laterally and assumed a chevron-shape and second, the palps became enlarged. The nukuloid tooth in multiple array forms an incredibly strong hinge and in some species it is impossible to open the shell wide without shearing the teeth. As consequence of this, the ligament has an elastic function to spring the valves open, but does not take on an 'anti shear' function. The palp, which in *Nucinella* collects filtered material from the gill, in the nukuloid collects deposited material direct from the sediment thus eliminating the gill as a food collector and processor. Particle processing becomes much less important as a part of function of the gill (although it is retained). The distal oral groove at the aboral limit of the palps is extended as a proboscoidal process. In this, the nukulid form, the inhalent respiratory flow into the mantle remains anterior. The shell remains stout and well calcified and is either triangular/ovate (*Nuculidae*), or rounded (*Pristiglomidae*) in shape.

As in the Lamellibranchia the change from an antero-ventral inhalent current to a posterior ingress was adopted early in the evolution of the Protobranchia and in like fashion involved the specialisation and eventual fusion of the posterior mantle margins to give rise to the predominantly siphonate nukuloids. Of these the Tindariidae is somewhat intermediate in form, in that while it has a posterior inhalent current as yet the posterior mantle margins are not fused to form a permanent aperture. Nevertheless, by apposition, an aperture is formed and is guarded by papillae developed from the mantle margin. This form is seen in no other protobranch group. In all other nukuloids the posterior mantle margin is enlarged to form a siphon, initially by the apposition later by the fusion of the mantle margins.

Consequent on the assumption of posterior ingress of water and particles into the mantle cavity, reorientation of the gill occurred as well as the separation (by mantle apposition) of a posterior feeding aperture below the inhalent aperture. This also involves specialisation and hypertrophy of the mantle margin.



As might be expected in a posteriorly siphonate bivalve, elongation occurs and the ovate, elongate and rostrate form with umbos, usually but not always, central or anterior in position, dominates the nuculanid groups. Once the basic nuculanoid shape had been achieved there was evolutionary radiation, much of which was related to habit. The overall general habitat remained the soft subtidal sediment and all genera retained their mobility. The foot remains well developed, muscular and active. Sediments vary as do feeding habits so that within the nuculanoid groups, there are surface, relatively slow moving, horizontal burrowers and rapid vertical burrowers with the consequent extremes of form represented by the moderately robust, tumid, ovate, non-gaping neilonellids and the fragile, slender, elongate, gaping yoldiids and sturdy, elongate, rostrate nuculanids and ledellids.

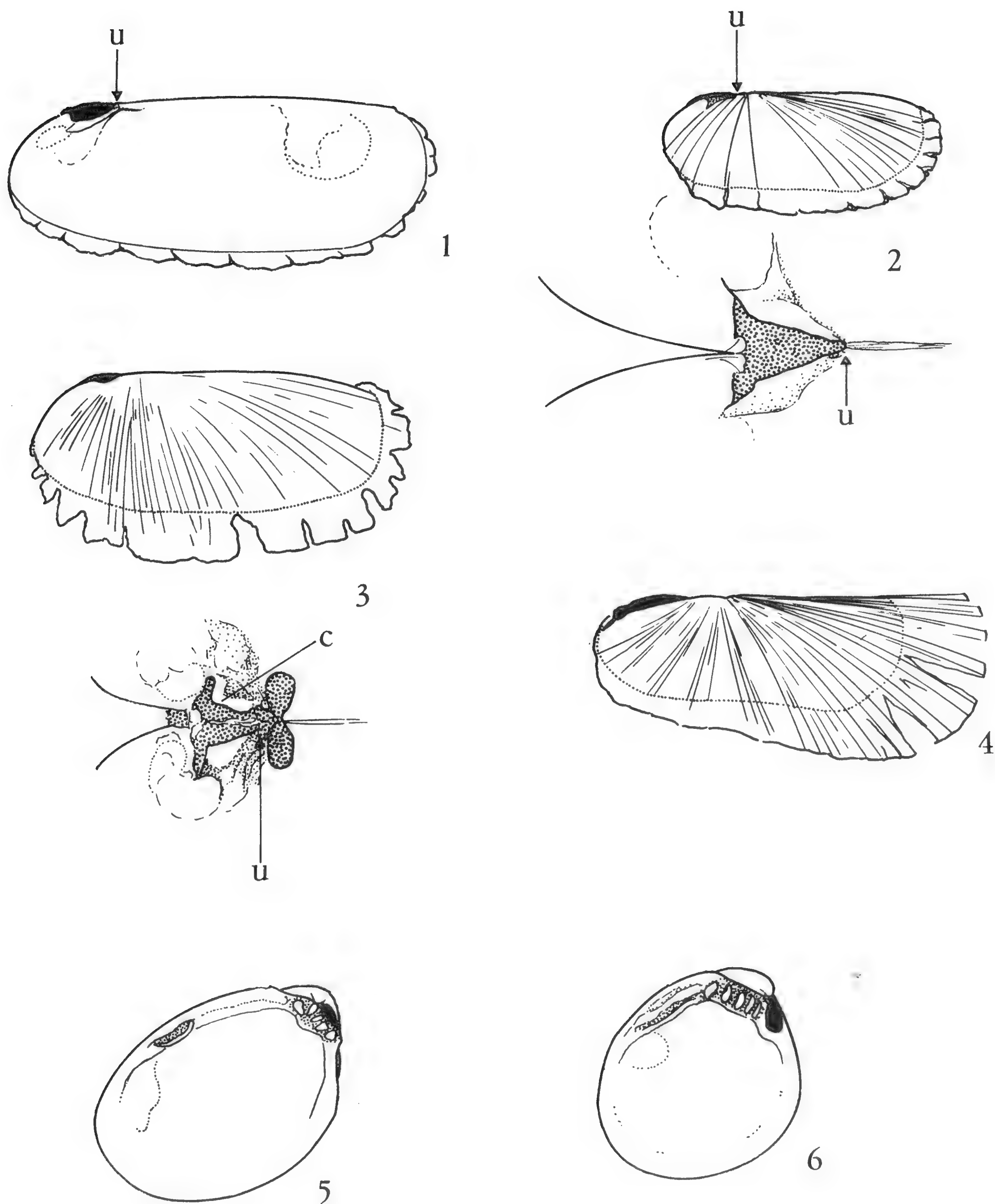
Apart from the proboscoid deposit-feeding mechanism probably the greatest restriction to radiation of form has been the persistence of the multiple, chevron-toothed hinge mechanism. While giving great protective strength it appears to have resisted modification. Twice, and each in a separate lineage, they have become modified to form elongate lateral teeth (*Lametilidae* and *Siliculidae*). Within the confines of the chevron, a lateral tooth can only be achieved by extending one arm of the V and suppressing the other. This is clearly seen in both *Prelametila* and *Propeleda*, which possess a mixture of short chevron, unequal chevron and lamellar teeth in the hinge series. Similarly, relatively few nuculanoid protobranchs have exploited the external ligament, even though it is present in the primitive tindariids. Only malletiids and spinulids possess well-developed elongate external ligaments. Both are rapid burrowers and presumably require strong, flexible, opening movement distributed *along the length of the dorsal margin of the shell*.

Brief mention must be made of shell sculpture and ornamentation. Again, there is marked conservatism within the Subclass. Concentric ridges predominate. They may be incised, with sharp edges or flat topped. They are frequently poorly defined and not particularly distinguishable from growth lines. Concentric sculpture is common throughout the Subclass and is not regarded as a highly significant taxonomic character (e.g. *Lamellinucula*, here, is not distinguished from *Nucula* s.s.). However other and much less common types of ornamentation have been accepted as distinguishing characters. For example carinae, radial ornamentation or oblique sculpture that is not coincident with growth lines such as is found in *Cnesterium*.

Despite their success, particularly in the deep sea where their digestive physiology has allowed them to exploit the refractile and impoverished organic material of the soft sediments, the protobranchs have been imprisoned by their feeding method and the conservativeness of their shell form. Not even modification of the hinge dentition (*Silicula*) has released them. Thus, despite a moderate degree of radiation which was established very early in the fossil record, these early forms remain conserved and are clearly recognisable to the present day.

#### ACKNOWLEDGEMENT

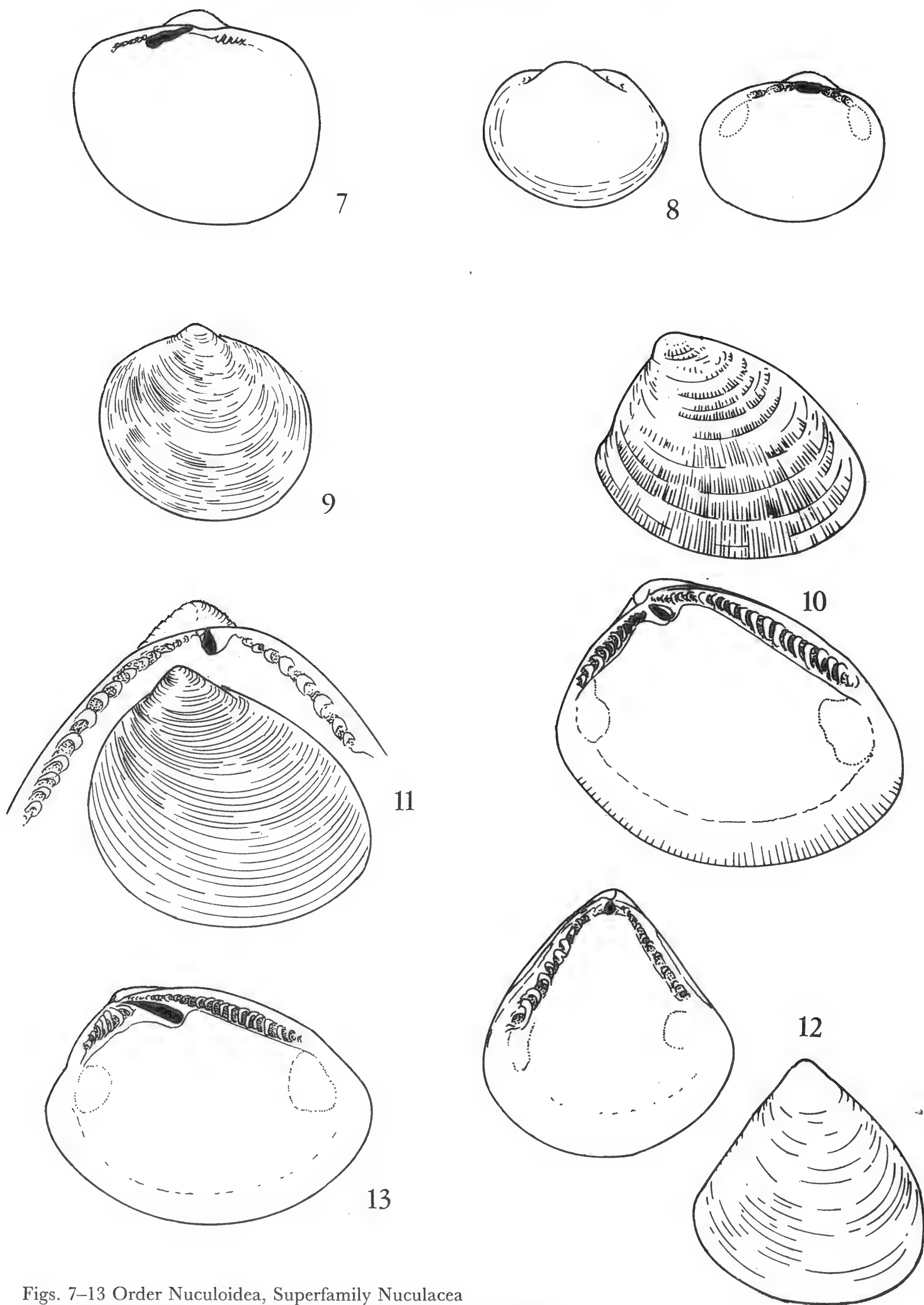
We would like to thank Mrs. Solene Morris, British Museum (Natural History) for her kind help and advice.



Figs. 1-6 Order Solemyoidea

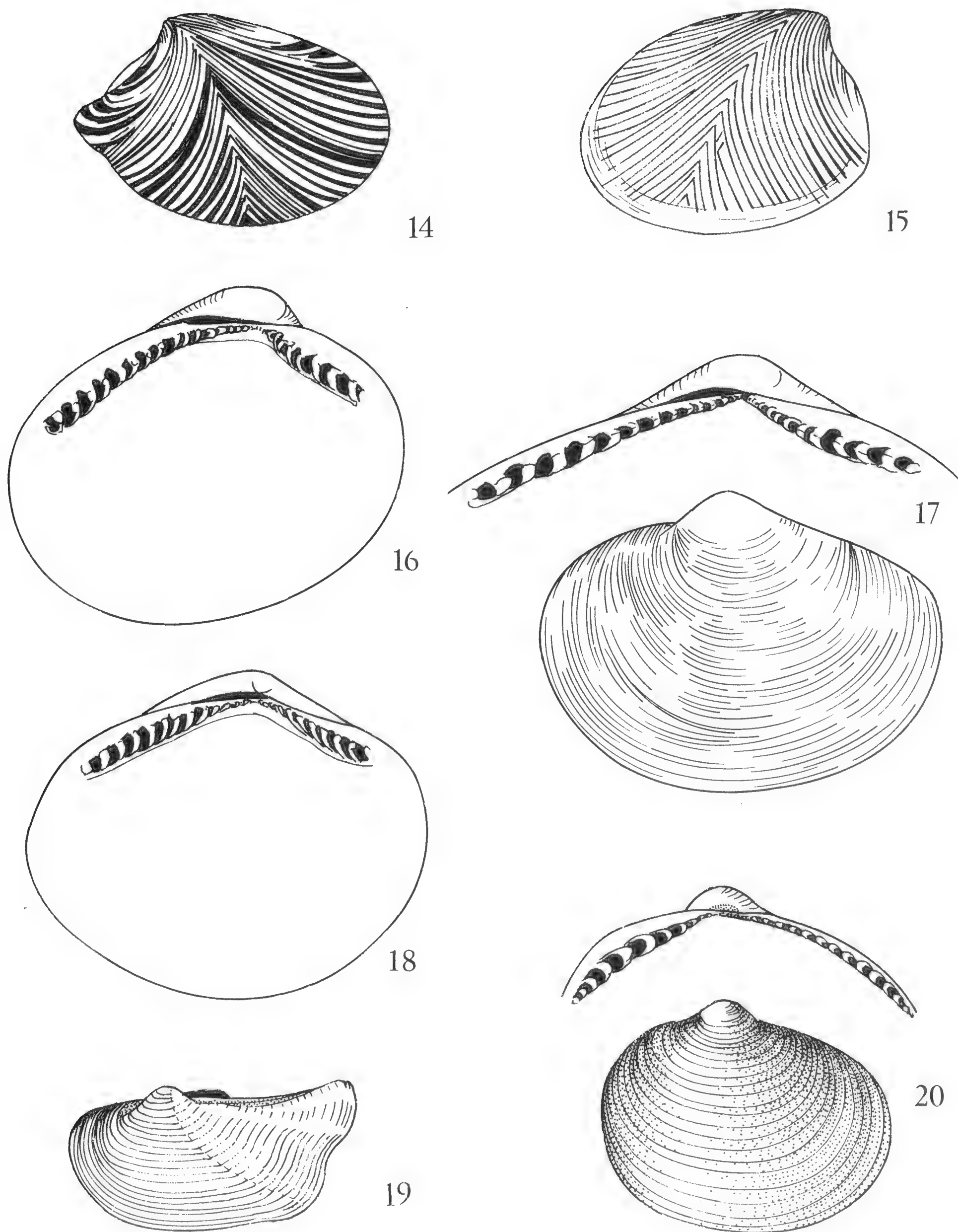
Family Solemydiae. 1, Subgenus *Solemya* (s.s.); 2, Subgenus *Petrasma* with internal view of the ligament; 3, Subgenus *Solemyrina* with internal view of ligament; 4, *Acharax*.

Family Nucinellidae. 5, Subgenus *Nucinella* (s.s.); 6, Subgenus *Huxleyia*. c. chondrophore; u, position of umbo.



Figs. 7-13 Order Nuculoidea, Superfamily Nuculacea  
 Family Pristiglomidae. 7, *Pristigloma*; 8, *Microgloma*; 9, *Pseudoglomus*.  
 Family Nuculidae. 10, Subgenus *Nucula* (s.s.); 11, Subgenus *Pronucula*; 12, Subgenus *Brevinucula*; 13, *Nuculoma*.





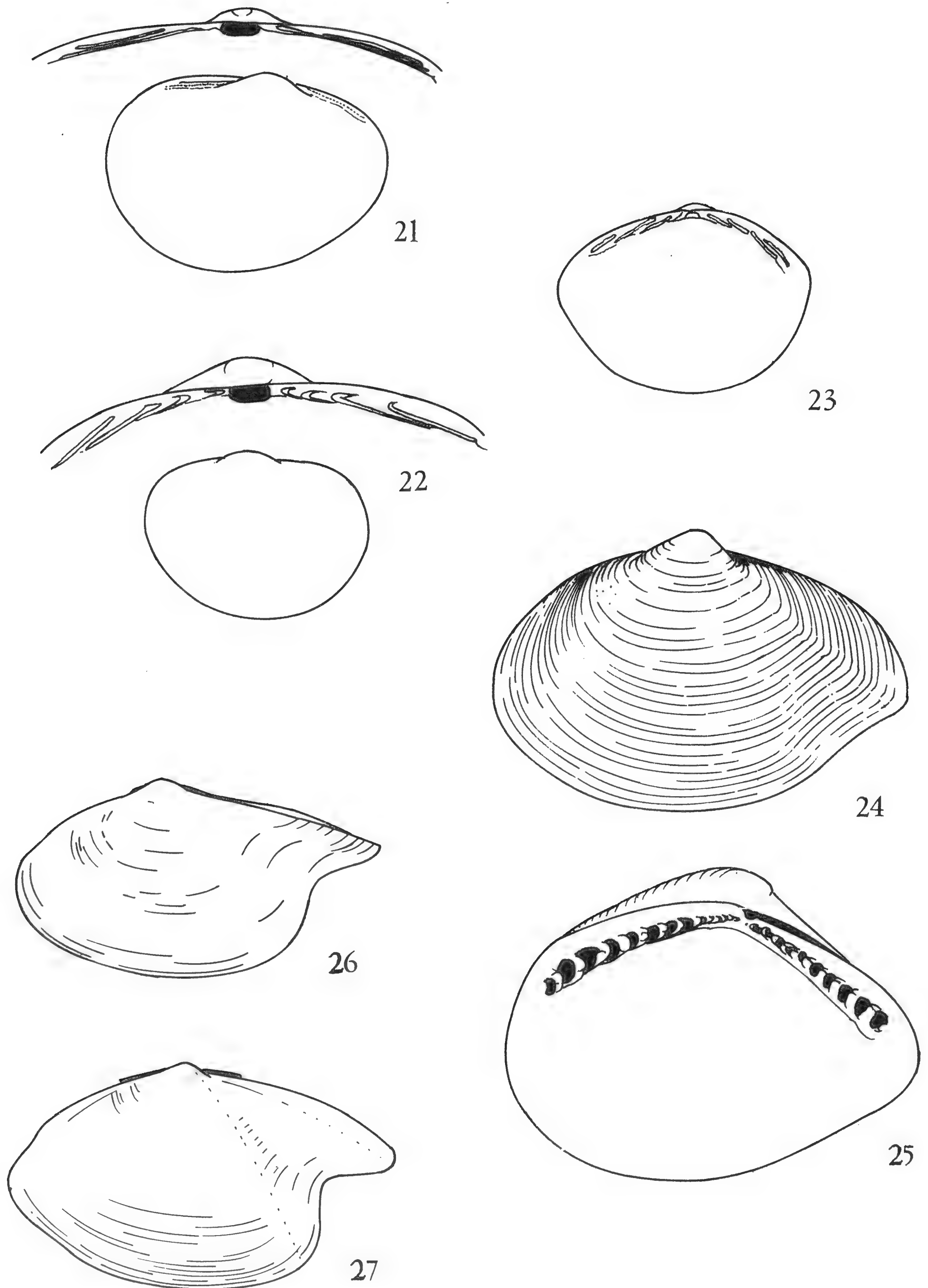
Figs. 14-20

Family Nuculidae continued. 14, Subgenus *Acila* (s.s.); 15, Subgenus *Truncacila*.

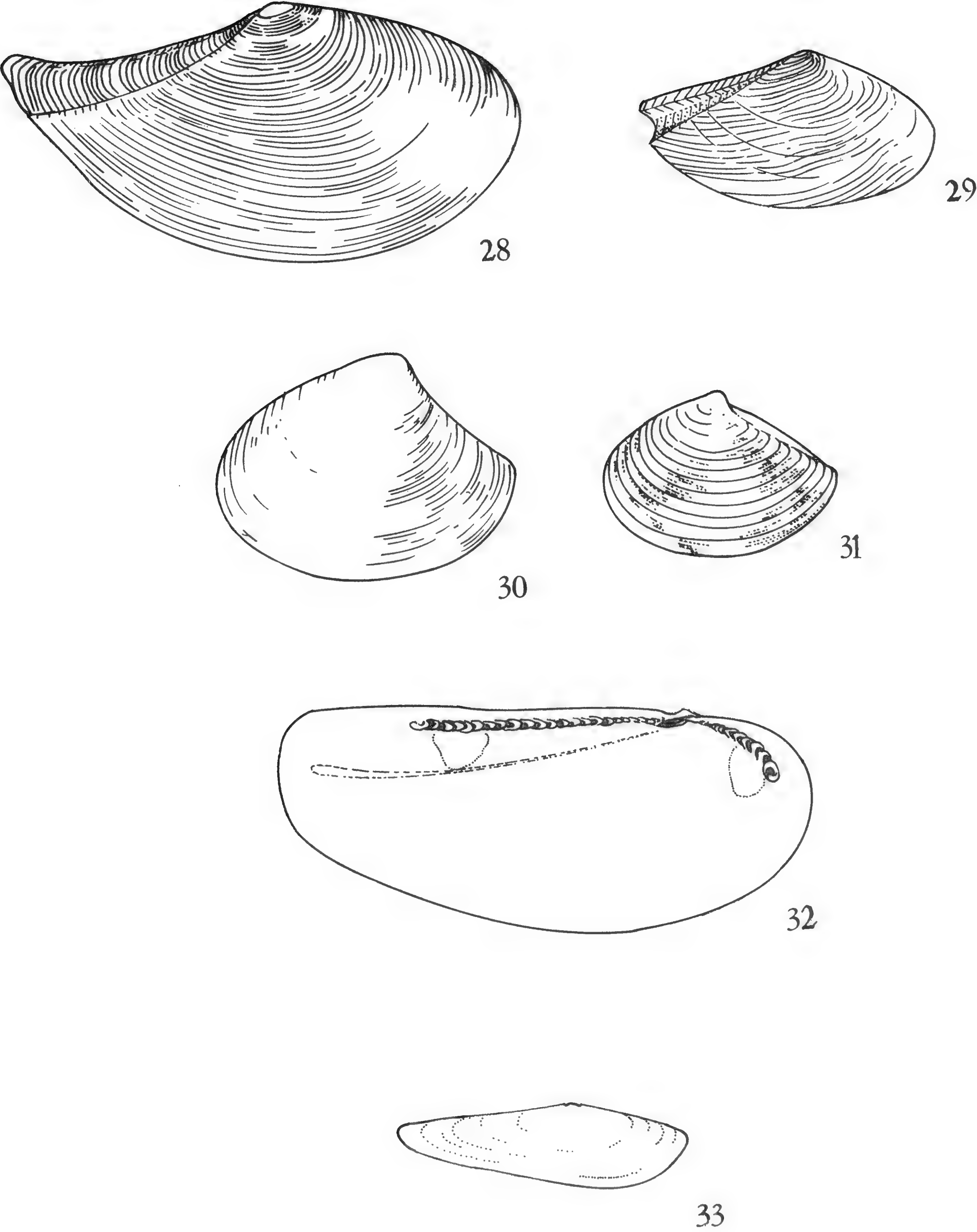
Superfamily Nuculanacea

Family Tindaridae. 16, *Tindaria*.

Family Saturniidae. 17, *Saturnia*; 18, *Pseudotindaria*; 19, *Neilo*; 20, *Protonucula*.

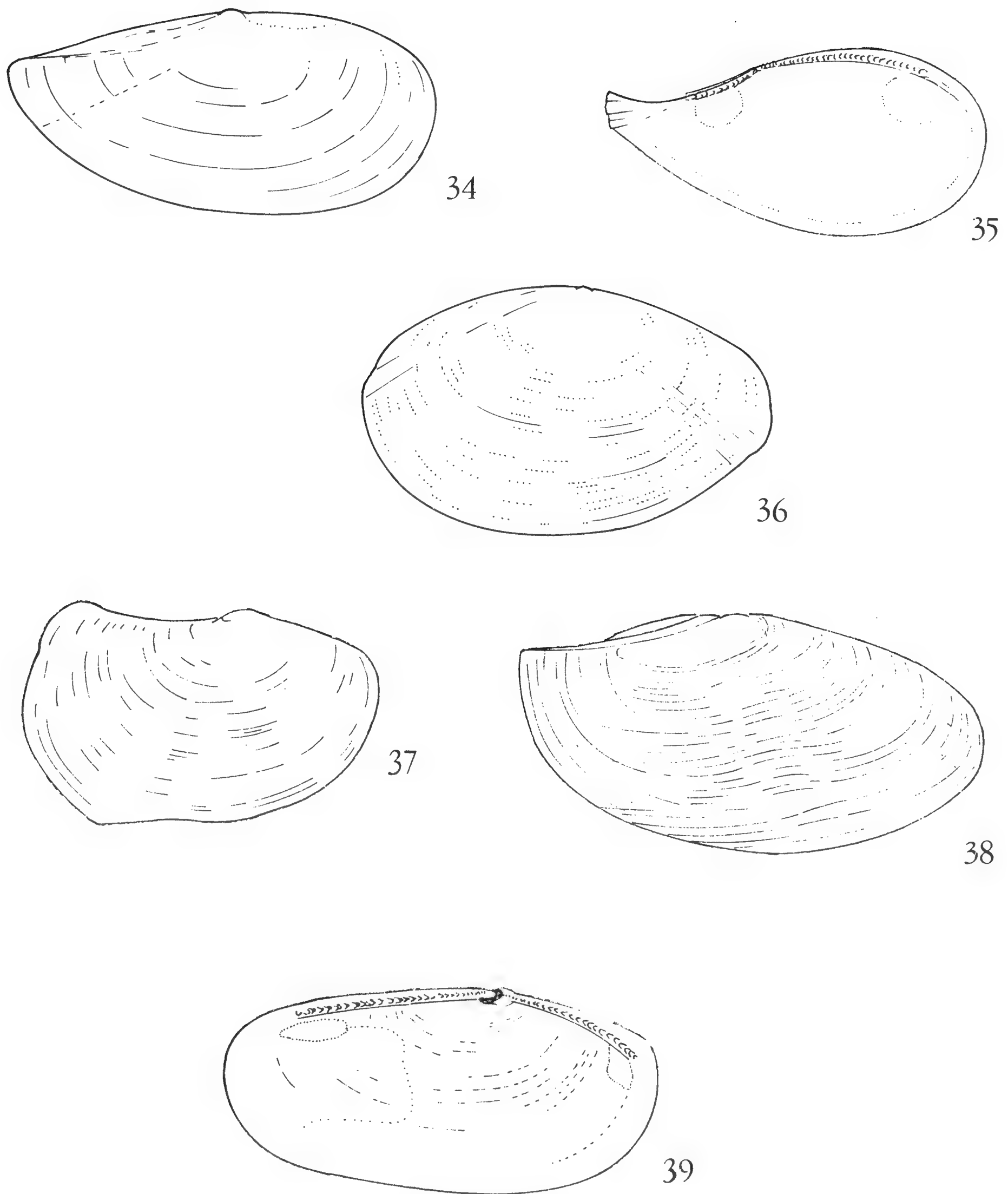


Figs. 21–27 Family Lametilidae. 21, *Lametila*; 22, *Prelametila*; 23, *Phaseolus*.  
Family Nuculanidae, Subfamily Ledellinae. 24, *Ledella*; 25, *Tindariopsis*. Subfamily Spinulinae. 26, Subgenus  
*Spinula* (*s.s.*); 27, Subgenus *Bathyspinula*.

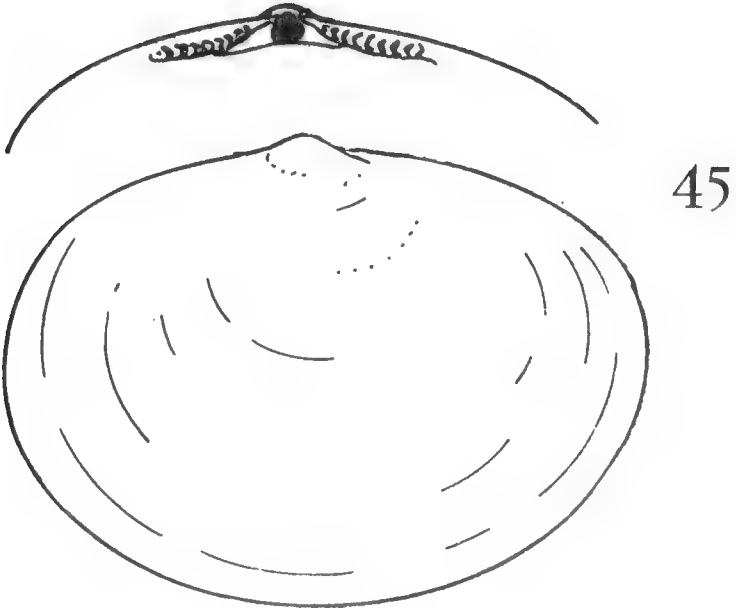
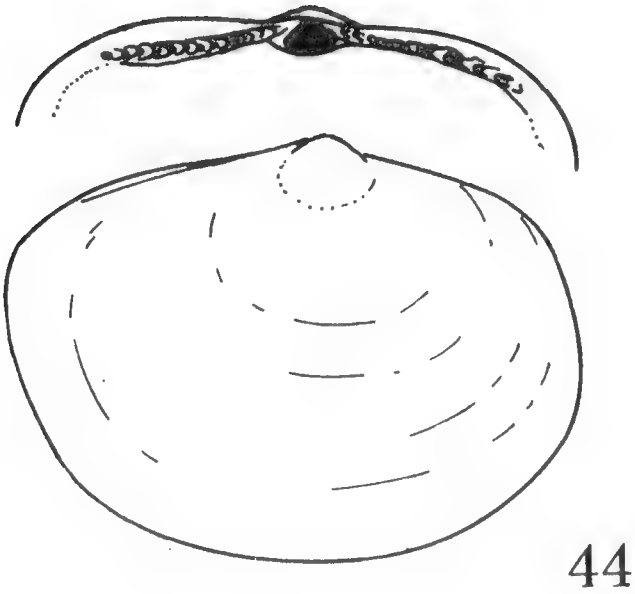
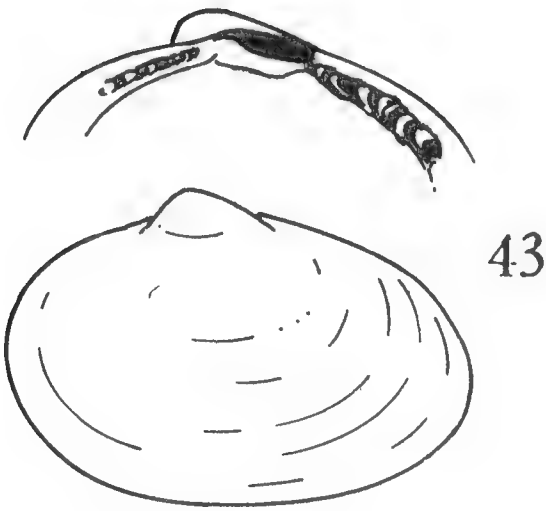
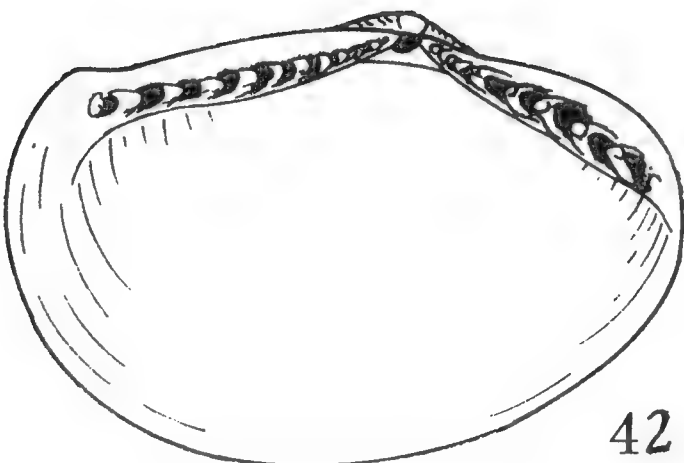
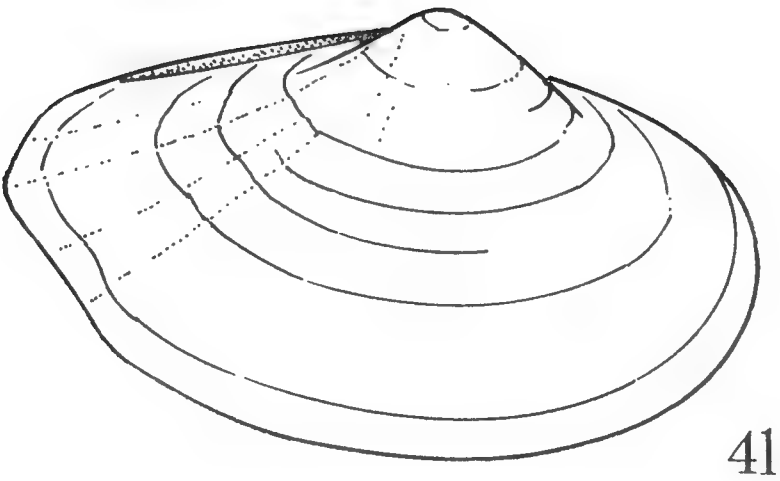
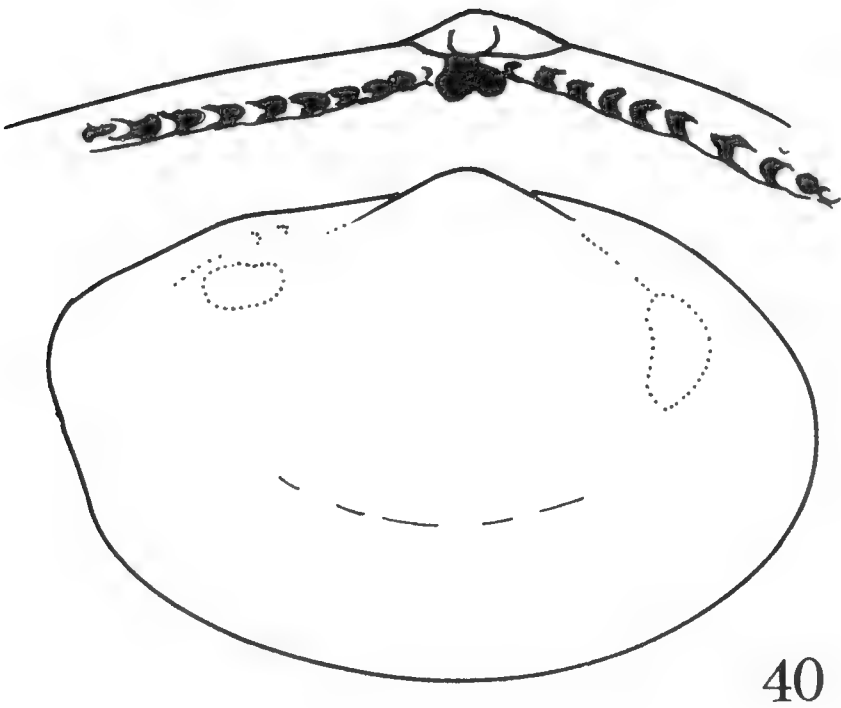


Figs. 28–33 Subfamily Nuculaninae. 28, Subgenus *Nuculana* (s.s.); 29, Subgenus *Lembulus*; Subgenus *Jupiteria*; 31, Subgenus, *Costanuculana*; 32 *Propeleda*, 33, *Adrana*.

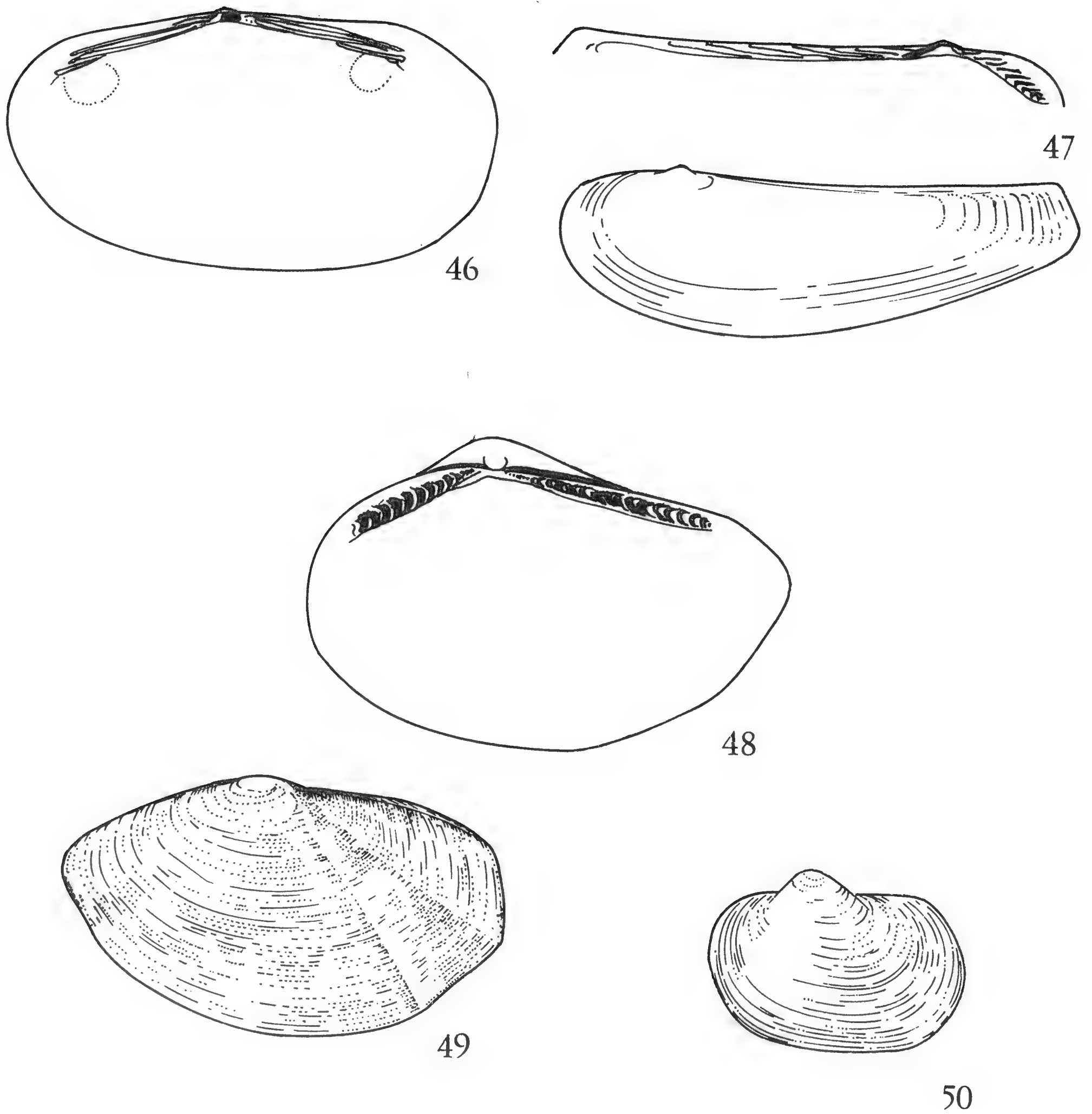




Figs. 34–39 Family Yoldiidae, Subfamily Yoldiinae. 34, Subgenus *Yoldia* (s.s.); 35, Subgenus *Kalayoldia*; 36, Subgenus, *Aequiyoldia*; 37, *Megayoldia*; 38, *Cnesterium*; 39, *Orthoyoldia*.



Figs. 40–45 Subfamily Yoldiellinae. 40, *Yoldiella*; 41, *Portlandia*; 42, *Adrenella*; 43, *Microyoldia*; 44, *Ovalea*; 45, *Serapta*.



Figs. 46–50 Family Siliculidae. 46, *Silicula*; 47, *Lamellileda*  
Family Malletiidae. 48, *Malletia*; 49, *Malletiella*; 50, *Minormalletia*.

GENERIC AND SUBGENERIC NAMES IN THE PROTOBRANCHIA

Names in bold type are described and figured herein, other names listed are synonyms.

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Costelloleda	232	Multidentata	234	Scissula	234
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# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## REPORT OF THE COUNCIL, 1985–1986

It is with regret that the Society has to report the deaths of the following 4 members; Mr. R. Macdonald, member since 1930; Dr. W. J. Clench, member since 1926; Dr. J. L. Bailey, life member since 1952 and Miss M. Jacques, member since 1979. The death of Mrs. Raffray, wife of the previous Treasurer was also announced.

The total membership of the Society now stands at 568, and is composed of the following categories:— Full members 430, Institutional members 38, Full life members 32, Family life members 6, Honorary members 6, Junior members 17, Family members 39.

*Resignations:* Full members 15, Institutional members 1, Family members 2, Junior members 1, Total 19.

*New members nominated & elected during 1985/6:* Full members 25, Institutional members 2, Family members 2, Junior members 4, Total 33.

*Struck off for non-payment of subscription:* Full members 27, Institutional member 1, Family members 2, Junior members 5, Total 35.

There were 3 transfers from Junior to Ordinary membership.

### *Meetings*

There were 7 Ordinary Meetings and 1 Annual General Meeting held in the Demonstration Room of the British Museum (Natural History). A Workshop to study British Marine small species was held in November at the Humfrey Rooms in Northampton, by courtesy of the Northamptonshire Natural History Society.

### *Publications*

Two parts of the *Journal of Conchology* were issued (Volume 32, parts 1 and 2). Four issues of the *Conchologists' Newsletter* were printed and issued with the Annual Programme Card of events. A list of amendments to the membership list was issued in June. One *Paper for Students* was issued:— '*An Introduction to Cephalopoda*' by C. P. Palmer.

### *Subscribers*

The total number of subscribers is 148 who took out a total of 162 subscriptions to the *Journal*. There were 11 subscribers to the *Conchologists' Newsletter* and *Papers for Students*.

### *Field Meetings*

Seven field meetings were held during 1985—April 5th to the 8th Weymouth, Dorset. May 25th Ipswich, Suffolk. June 9th Northampton. July 14th Linslade, Beds. July 27th Folkestone, Kent. September 14th Leicester and September 28th Haslemere, West Sussex. Thanks are due to the following for leading these meetings—Mr. G. D. Saunders, Mr. I. J. Killeen, Mr. A. G. H. Osborn, Mrs. E. B. Rands, Dr. A. J. Rundle, Mr. D. Guntrip, Mr. S. P. Dance, Mr. J. H. Mathias and Dr. M. J. Willing.

J. D. NUNN  
(Hon. Secretary)

## TREASURER'S REPORT, 1985

The accounts for 1984 show a deficit of £417.86. This is not in itself a serious matter, as included in the expenses is the payment of £550 for covers for the *Journal of Conchology* which relates to the whole of Volume 32 taking in the years 1986 and 1987.

Nevertheless there has been a steady increase in costs mainly in printing and meeting charges (now £55 for hire of room at the British Museum of Natural History, with the likelihood of further increase). It is also hoped to resume regular publication of *Papers for Students*. The present subscription rate has been unchanged for five years, and as Members will know an increase is now proposed which it is hoped will not require amendment for some considerable time.

There is again a fall in income from Members' subscriptions, and also in payments from Subscribers. Happily there is a substantial rise in the investment income.



Covenanted subscriptions produced the welcome addition of £258.66. The Society is grateful to all Members who pay in this way, and would be glad if other Members would consider this form of payment.

14 Ordinary Members. 2 Family Members and 2 Junior Members are in arrears with 1985 subscriptions. Members are reminded that no further publications can be sent to those whose current subscriptions remain unpaid.

I regret that the exceptionally severe weather has prevented the Auditors (both of whom are obliged to cross the Pennines) from completing the audit, and I am therefore obliged to ask the meeting to accept the accounts subject to the Auditors' subsequent satisfaction.

MARJORIE FOGAN  
Hon. Treasurer

#### RECORDER'S REPORT: MARINE MOLLUSCA

Among many new reports which will be included in a forthcoming *Conchological Society* paper of additions and amendments to the *Sea Area Atlas*, the following are of particular interest:

*Truncatella subcylindrica* (L.) has been found living in Pagham Harbour, West Sussex, (S15, SZ89), in 1977 and 1983, by Dr. M. B. Seddon and Dr. D. T. Holyoak. This appears to be its only remaining site in Britain besides the Fleet in Dorset (S16), as the gravel pit site near Shoreham described by A. E. Ellis in 1932 (*Proc. Malac. Soc.* XX, p. 16) apparently no longer exists.

*Circulus striatus* (Philippi). One living among small algae from the lower shore at Lannacombe Beach, South Devon, (S18, SX83), in 1985 (D. R. Seaward, confirmed Dr. V. Fretter and Mrs. S. M. Turk). This is the only live post-1950 record for the British Isles.

*Cuthona genovae* (O'Donoghue). This Mediterranean sea slug has been found in Lough Ine in South West Ireland (S37), (Wilson and Picton (1983) *Ir. Nat. J.* **21**, p. 70).

*Cumanotus beaumonti* (Eliot). Diving surveys by B. E. Picton for the Ulster Museum have recently shown this sea slug to be present off the East coast of Ireland in areas S27, S28 and S29a. According to Thompson and Brown (*Biology of Opisthobranch Molluscs*, vol. 2, 1985), it was only previously known from Norway and the Plymouth area.

D. R. SEAWARD

#### RECORDER'S REPORT: NON-MARINE MOLLUSCA

##### A. Grid mapping

Very good progress continued to be made during 1985. The systematic work of Mr A. O. Chater and Mr A. P. Fowles in Cardigan and Mr I. K. Morgan in Carmarthen is transforming our knowledge of a hitherto poorly studied part of the highland zone. Mapping in the upper Severn valley west of Birmingham by Mrs M. Fogan and Mrs E. B. Rands in the summer of 1985 also filled many gaps in what is a difficult area for molluscs.

Systematic extraction of all usable old records for the new edition of the *Atlas* is now largely complete, including the gridding of data from the Society's Census notebooks (1876 onwards) and the species notebooks compiled by J. W. Taylor and W. D. Roebuck and held in the Department of Zoology, BMNH. The *Journal of Conchology* has also been searched.

##### B. Vice-comital records

An unusually large number of new records have been verified since the last report (*J. Conch., Lond.*, **32**, p. 143). Unless stated otherwise, all date from 1985–6.

Dorset (9): *Boettgerilla pallens*, Hilfield Hill (31/6304), D. R. Seaward.

Hants South (11): *Limax maculatus*, Christchurch (40/19), Charles Ashford, 1884 (identification based on an unpublished dissection drawing).

Sussex West (13): *Boettgerilla pallens*, Duncton (41/9616), A. O. Chater.

Herts (20): *Gyraulus laevis*, Amwell (52/3713), Mrs E. B. Rands: *Ferrissia wautieri*, St. Albans (52/1204; lily pond), D. Guntrip.

Suffolk West (26): *Deroceras caruanae*, Great Cornard (52/8839), I. J. Killeen.

Bedford (30): *Limax valentianus*, Sandy (52/1649; nursery garden); *Pisidium pulchellum*, R. Ouzel, Heath and Reach (42/9127), Mrs E. B. Rands and D. Guntrip.

Hunts (31): *Deroceras caruanae*, Water Newton (52/1097), Mrs E. B. Rands.

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

	£	£	£
Publications:—			
Newsletter .....		2,763.07	4,882.52
Paper for Students .....		154.52	2,819.52
			<u>40.00</u>
			7,742.04
Journal:—			72.21
Volume 32 No. 1 .....	2,908.10		
Volume 32 No. 2 .....	3,071.61		
Covers for Volume 32 .....	<u>550.00</u>		
Members List		6,529.71	43.00
			50.65
		155.07	17.50
			13.50
			9.00
Printing, Stationary and Postage		587.51	12.85
Officers' Expenses .....		376.61	9.50
Meetings .....		272.50	5.00
Subscriptions .....		8.00	98.35
Bank Charges .....		10.18	
Marine Workshop .....		85.00	259.35
Lemche Books ordered for			97.50
Members .....		208.00	156.00
			2,013.23
			391.98
			<u>357.85</u>
			2,763.06
Transfer to Reserve and Research			
Fund .....			<u>357.85</u>
			2,405.21
			<u>10,732.31</u>
			417.86
			<u>£11,150.17</u>
Net Loss for the Year .....			
		<u>£11,150.17</u>	



- Northampton (32): *Ferrissia wautieri*, Cosgrove (42/7942), Mrs E. B. Rands and D. Guntrip; *Milax gagates*, Yardley Hastings (42/8657), Mrs E. B. Rands; *Boettgerilla pallens*, Bozenham Mill (42/7648), A. J. Rundle.
- Salop (40): *Milax gagates*, Morbrook (32/6991); *Boettgerilla pallens*, Coalbrookdale (33/6604), Mrs M. Fogan and Mrs E. B. Rands.
- Brecon (42): *Vallonia costata*, island in Llangorse Lake (32/12), C. Oldham, 1907.
- Radnor (43): *Vallonia costata*, Glasbury (32/13), J. W. Vaughan, 1905. [This and the preceding record were inadvertently omitted from the Census summary published in *J. Conch., Lond.* **31** (1982) p. 67]
- Carmarthen (44): *Vertigo antivertigo*, Cil-y-blaidd, Pencarreg (22/5445); *Vertigo lilljeborgi*, Cil-y-blaidd, Pencarreg (22/5446), both A. O. Chater; *Vallonia costata*, Ferryside (22/3609); *Boettgerilla pallens*, Pentregwenlais (22/6016); *Balea perversa*, Pontnewydd, Kidwelly (22/4407); *Monacha cantiana*, Llanelli (21/4999); *Anodonta anatina*, R. Tywi, Dryslwyn (22/5620), all I. K. Morgan.
- Cardigan (46): *Milax gagates*, *Boettgerilla pallens*, Aberystwyth (22/5880); *Ceciloides acicula*, Llechryd (22/2143), all A. O. Chater; *Limax tenellus*, Gwenffrwd valley (22/5960), A. O. Chater and A. P. Fowles.
- Nottingham (56): *Deroceras caruanae*, Beeston (43/5336), D. T. Holyoak and M. B. Seddon.
- Chester (58): *Helicodiscus singleyanus*, Burton (33/3174; garden), C. R. C. Paul.
- Lancaster South (59): *Arion 'lusitanicus'* (Quick's form), Atherton (34/6804), Mrs M. Fogan.
- York North-east (62): *Abida secale*, Helmsley (44/68), H. Teetham, 1890 (Leicester Museum); *Boettgerilla pallens*, Appleton-le-Moors (44/7487), A. Norris.
- York South-west (63): *Deroceras agreste*, South Anston (43/5283), A. Norris.
- Cheviotland (68): *Milax budapestensis*, Tweedsmouth (36/9952), Mrs M. Fogan.
- Westmorland (69): *Vallonia pulchella*, Allithwaite (34/3875), Mrs D. K. Marriott.
- Isle of Man (71): *Arion fasciatus*, Onchan (24/4078), Miss S. M. Davies, 1984.
- Dumfries (72): *Pyramidula rupestris*, Hoddum (35/1672); *Limax maculatus*, Powfoot (35/1465), both A. O. Chater.
- Lanark (77): *Anodonta cygnea*, Possil Marsh, Glasgow (26/56), ca 1970 (Glasgow Museum).
- Edinburgh (83): *Limax maculatus*, Edinburgh (36/2474), A. T. Sumner.
- Perth Mid (88): *Bithynia leachii*, Dunmore Loch, Pitlochry (27/9258), A. Pike, 1984; *Cochlodina laminata*, Old Wood of Methven (37/0526), Mrs D. K. Marriott.
- Forfar (90): *Limax tenellus*, Tarfside, Glen Esk (37/4979); *Deroceras agreste*, Aughranie, Glen Esk (37/4480), both A. O. Chater; *Anodonta anatina*, Belgavies Loch (37/5350), C. Riddell and N. K. Atkinson.
- Kincardine (91): *Valvata piscinalis*, Loch Saugh (37/6778); *Pisidium subtruncatum*, *P. nitidum*, Loch Wee, Edzell (37/6269), all N. K. Atkinson, 1984; *Arion fasciatus*, *Milax sowerbyi*, Banchory (37/7095); *Limax cinereoniger*, Hill of Tillylair (37/6394); *Deroceras laeve*, Loch of Leys (37/6997), all A. O. Chater.
- Aberdeen South (92): *Milax sowerbyi*, Old Aberdeen (38/9308), A. O. Chater.
- Aberdeen North (93): *Milax gagates*, *M. budapestensis*, Boddam (48/1342), A. O. Chater.
- Easternness (96): *Deroceras agreste*, Rothiemurchus (28/8908), A. O. Chater.
- Westernness (97): *Vertigo pusilla*, 'Dark Mile', Loch Arkaig (27/1888), Mrs D. K. Marriott, 1984.
- Ross West (105): *Arion 'lusitanicus'* (Quick's species), Gairloch (18/8076), A. T. Sumner.
- Sutherland West (108): *Milax gagates*, Balnakeil (29/3967), R. C. Preece.
- Caithness (109): *Margaritifera margaritifera*, Bridge of Forss (39/0368), R. G. Meiklejohn.

The more interesting of these records are as follows:

*Bithynia leachii*. This is a surprising find in Perthshire. The only other Scottish populations of this essentially lowland species are in canals in the midland valley. Dunmore Loch is said to be artificial and the species may be a recent introduction here.

*Ferrissia wautieri*. There are still fewer than a dozen records of this introduced limpet, first noted in Britain in 1976. Probably it remains overlooked and will be found elsewhere in the English lowlands if specially searched for.

*Vertigo lilljeborgi*. Since the find of a colony of this relict boreal snail in Cardigan in 1984 (*J. Conch., Lond.*, **32**, p. 147) further sites have been detected by Mr Chater in the same general area along the upper Teifi valley in Cardigan and Carmarthen. At Pencarreg (v.c. 44) the habitat is a *Juncus* marsh in an abandoned floodplain ox-bow.

*Abida secale*. The occurrence in N. E. Yorkshire represents a considerable extension of known range. The specimens, dated 1890, were clearly live-collected. Judging from other material in Leicester Museum ascribed to the same collector (in the A. Smith collection) Henry Teetham lived in York and was active in the years around 1900.

*Helicodiscus singleyanus*. The discovery in Cheshire is the fifth known from an open site in Britain and the most northerly. Numerous fresh shells were found in a garden, at the foot of sandstone terraces constructed about 1930. The strong presumption remains that this subterranean snail is an introduction in the British Isles.

*Boettgerilla pallens*. The seven additional vice-county records demonstrate the continuing rapid spread of this slug.

*Limax maculatus*. The discoveries in Dumfries and Edinburgh are the first from the Scottish mainland. That from Hampshire is the first from southern England (and also the earliest certain evidence for the presence of this possibly introduced species in the British Isles).

*Limax tenellus*. It is gratifying to be able to include two entirely new vice-comital records for this old woodland rarity. The habitat in Cardigan is a coppiced sessile oak wood, that in Forfar a mixed wood of Scots pine and birch.



*Limax valentianus*. This Iberian slug, long known from British greenhouses, was first reported from an open site (near Dublin) in 1981 (*J. Conch., Lond.*, **31**, p. 132). The new find in a nursery garden in Bedfordshire is the first in England. It seems likely that the species is establishing itself locally in disturbed habitats, as in several other north European countries.

*Deroceras agreste*. The discovery in south Yorkshire (v.c. 63) is of interest in helping to link the main area of distribution in Scotland and the northern Pennines with the very isolated populations in the Norfolk Broads. The habitat at south Anston is limestone grassland.

Not included in the above list are Mr D. Guntrip's discoveries of *Toltecia pusilla* in nurseries in Buckinghamshire (v.c. 24) and Bedfordshire (v.c. 30) (*J. Conch., Lond.* **32** p. 200). Although in the open, the habitats are of such an artificial character (gravel on polythene sheeting) that the species cannot yet be considered as properly naturalised in England, though it may become so.

Finally, although not new to its vice-county, Mr D. C. Long's rediscovery of *Lauria sempronii* in West Gloucestershire (v.c. 33) is of outstanding interest in demonstrating the continuing presence of the species in the British Isles (*J. Conch., Lond.*, **32**, p. 201).

M. P. KERNEY

## COMMUNICATIONS

### NOTES ON SOME LAND GASTROPODA FROM MADEIRA

During a visit to the island of Madeira in December 1984 the following land snails were collected that are apparently either rare or unrecorded there.

*Assiminea eliae* Paladilhe c. 2.5 km E. of Ponta do Sol, S. Madeira; numerous, living with *Truncatella subcylindrica* (L.), *Pseudomelampus exiguus* (Lowe) and *Ovatella myosotis* (Draparnaud), on inland edge of boulder beach under mats of *Atriplex*. The shells are much larger (height c. 3.3 mm) with a longer more pointed spire than in *A. littorina* (Delle Chiaje), the only species of Assimineidae hitherto recorded from the Madeiran Islands. The shell form and size closely match descriptions and figures of *A. eliae* given by Germain (*Faune de France*, **21** (1930) pp. 595–596) and Backhuys (*Zoogeography and Taxonomy of the Land and Freshwater Mollusca of the Azores*, Backhuys & Meesters (1975), pp. 50–51). *A. recta* (Mousson) from Mogador (=Essaouira, Morocco) has an even larger and more slender shell (specimens in National Museum of Wales). *A. eliae* was originally described from SW. France and has been recorded also from Spain, Portugal and the Azores. However, the genus includes numerous nominal species from as far away as SE. Asia and S. Africa and a comprehensive systematic revision may be necessary to reliably establish how many species are involved and their distribution.

*Discocharopa aperta* (Möllerndorff) E. side of Ponta da Cruz (SW. of Funchal), S. Madeira; one shell was found beneath a boulder on a grassy slope above sea-cliffs at c. 25 m above sea level. The only previous record of this tiny Pacific Ocean species of Charopidae from Madeira was of two shells from c. 2 km S. of Machico, E. Madeira (Gittenberger & Ripken, *Basteria*, **47** (1983) p. 58).

*Oxychilus alliarius* (Müller) Thirty-nine were collected by EN-101 road c. 2 km E. of Arco de São Jorge, N. Madeira. They were living on rocky slopes and crags with herbs on ledges and some shade from bushes and *Eucalyptus* trees, at c. 125 m above sea level. This is apparently the first Madeiran record of this widespread NW. European species.

*Cernuella vestita* (Rambur) E. side of Ponta da Cruz (SW. of Funchal), S. Madeira; many living snails were collected from piles of rotting banana (*Musa* sp.) leaves on grassy edge of plantation, at c. 50 m above sea level. The shell characters are typical of *C. vestita*, a W. Mediterranean and Iberian species previously unrecorded on Madeira. In addition, dissection has established that the distal genitalia resemble those figured for this species by Manga Gonzalez (*Los Helicidae (Gastropoda, Pulmonata) de la Provincia de León*, (1983) (León, p. 178, Fig. 12), in having epiphallus somewhat longer than the penis; flagellum 1.5×penis length; one large dart sac with dart, another much smaller (lacking dart) joined to its inner (vaginal) side.

Thanks are due to the staff responsible for the Collections of Mollusca at the British Museum (Natural History) and the National Museum of Wales for helpful access to specimens in their care.

M. B. SEDDON\*, B. COLES, B. COLVILLE, D. T. HOLYOAK AND R. C. PREECE

\*Department of Geography, University of Nottingham, Nottingham NG7 2RD

(Received, 15th April 1986)

### NOTES ON SOME LAND GASTROPODA FROM THE PYRENEES AND N. SPAIN

Various distributional records of Mollusca collected recently appear to be extensions of known ranges. In the list below, the UTM 10 km grid reference is given in parentheses.

*Acicula cryptomena* (Folin & Bérillon) June 1985, five living animals found under dead wood in carr woodland by stream near Pont de Crabiou, E. of Pragnères, Hautes-Pyrénées, France, at 1270 m ASL (BH51), Coll. PT; June 1985, one live animal in moist leaf-litter in beech (*Fagus sylvatica* L.) woodland above river low on S. side of valley, on Sierra de las Cutas, Ordesa National Park, Prov. Huesca, Spain, at c. 1400 m ASL (YN32), Coll. PT. There are apparently no other published records of *A. cryptomena* from so far east in either France or Spain. Three other snail species that are very local in N. Spain were collected by PT at the same locality in the beech woodland of Ordesa National Park: *Cochlodina laminata* (Montagu), *Clausilia dubia* Draparnaud and *Ciliella ciliata* (Studer); these were reported from this region by Altimira & Balcells (1972, *Pirineos*, Jaca **104** (1972) pp. 15–81).

*Cryptazeca kobelti* Gittenberger 26 Aug. 1984, 23 living animals and 43 empty shells (along with three shells of *C. vasconica* (Kobelt)) found in damp leaf-litter and moss in heavy shade of moist beech woodland on steep limestone hillside by N625 road c. 3 km S. of Orduna, Prov. Alava, Spain (VN95), Colls. DTH, MBS and M. Holyoak.

When Gittenberger (*Zool. Meded., Leiden* **57** (1983) p. 313) named this species it was known from only four shells collected about 1894 by Kobelt: 'some Dutch malacologists looked for it near Orduna, but in vain'. Kobelt reported that he found his four shells on grassy slopes, a very different habitat to the moist woodland in which it was rediscovered.

*Arion intermedius* Normand 5 July 1984, shaded limestone rocks in Gorges du Rebenty, by D107 road 1.5 km SW. of Merial, Aude, France (DH13), 1105 m ASL, Colls. DTH & MBS; 5 July 1984, shaded limestone slopes by N152 road 5 km NW. of Ripoll, Prov. Gerona, Spain (DG 38), 800 m ASL, Colls. DTH & MBS. There has been considerable uncertainty about the occurrence of this species in the E. Pyrenees (cf. Kerney, Camerón & Jungbluth *Die Landschnecken Nord- und Mitteleuropas*, Parey (1983), map 142); it was not listed for Catalonia by Haas (*Trabajos del Museo de Ciencias Naturales de Barcelona* **13** (1929)), but Altimira & Balcells (1972, *op. cit.*) gave a record from Prov. Huesca.

*Oxychilus* cf. *altimirai* Riedel 25 Aug. 1980, 4 km up road to Col du Couret from Bagnères, Hte.-Pyrénées, France (BH76), Coll. DTH. The single shell (resembling shells of *O. helveticus* (Blum) but with a smaller umbilicus) is a good match for illustrations of this species, which was described from Prov. Huesca, Spain (Riedel, *Ann. Zool., Warszawa* **29** (1972) p. 126; see also Riedel in Altimira & Balcells (1972) *op. cit.*, p. 45). However, additional shell and anatomical material needs to be studied both to confirm the distinctness of *O. altimirai* and to establish that it occurs on the French side of the Pyrenees.

*Bofilliella subarcuata* (Bofill) 24 Sept. 1984, fresh shells from under ivy *Hedera helix* L. on limestone ledge, by road 2 km W. of Santa Pau, near Olot, Prov. Gerona, Spain (DG66), Coll. SPD. Another record of this uncommon Catalanian endemic from an open site, as opposed to a cave entrance or spring (cf. Holyoak & Seddon, *J. Conch., Lond.* **32** (1985) p. 68). Several visits to the type locality, at Llado, near Figueras, Prov. Gerona, by SPD, DTH and MBS in 1983 and 1984 failed to turn up this species, which may be in decline.

*Cochlodina laminata* (Montagu) 29 June 1984, in moss and wet logs in small wood below El Portillon, SW. of Bosost, Catalonia, Spain (CH03), 1100 m ASL, Coll. SPD. This species is apparently rare in the Spanish Pyrenees, at the south-western limit of its range (cf. Haas 1929, p. 327; Altimira & Balcells 1972, *op. cit.*).

*Clausilia dubia* Draparnaud 26 June 1984, one fresh shell from wooded valley at Molins del Sispony, Andorra (CH71), Coll. SPD. It is rare in the Spanish Pyrenees (Haas 1929, p. 331; Kaufel, *Senckenbergiana* **11** (1929) p. 21; Altimira & Balcells 1972, *op. cit.*).

*Mastigophallus rangianus* (Férussac) 16 Sept. 1984, fresh shells from around monastery (amongst masonry, ivy, dead leaves and grasses), San Pedro de Roda, near Rosas, Costa Brava, Spain (EG18), 500 m ASL, Coll. SPD; 16 Sept. 1984, one dead shell from dry soil at foot of rampart of Castell Carmanso, near Rosas, Costa Brava, Spain (EG18), Coll. SPD; 26 Sept. 1984, old shells from debris in small quarry by Rosas-Cadaques road, 2 km W. of Cadaques, Spain (EG28), Coll. SPD. This distinctive species is endemic in a small region near the coasts of Pyrénées-Orientales (France) and adjoining parts of NE. Spain. Haas (1929, p. 243) did not know of any Spanish records since that from 'Catalonia' by M. P. Graells (*Cat. mol. terr. y ag. dul. Espana*, 1846); Graells's specimens are not in the Zoological Museum of Barcelona, which houses his collections (Sra. Roser Nos, pers. comm. to SPD). More recently, it was reported from near Cadaques by Altimira (1960, *Miscelanea Zoologica*, Barcelona **1**, p. 25; 1968, *ibid.* **2**, p. 13).

S. P. DANCE, D. T. HOLYOAK<sup>1</sup>, M. B. SEDDON AND P. TATTERSFIELD

<sup>1</sup>Department of Geography, University of Nottingham, Nottingham NG7 2RD

(Received, 24th April 1986)

### THREE SCAPHOPODS NEW TO THE BRITISH MARINE FAUNA

Between 1970 and 1976 the Scottish Marine Biological Association's research vessel 'Challenger' collected benthic material from the Rockall Trough, west of Scotland. While examining the scaphopods, sent to me for identification, I was able to report that three of them were entirely new to the British marine fauna. One was previously described by Jeffreys, the other two appear to be undescribed. This is a preliminary notice, prior to full description and naming of the two undescribed species.

#### **Siphonodentalium teres** (Jeffreys, 1882).

*Proc. Zool. Soc. London* for 1882, p. 661, pl. 49, Fig. 5.

This species was briefly reported in *Conchologists' Newsletter* no. 61, pp. 3, 4 (1977). Jeffreys described specimens dredged by 'Porcupine' Expedition in 1870 from about 60 miles NNW of Lisbon, Portugal. Thereafter there were no records until SMBA 'Challenger' discovered it in the Rockall Trough during September 1973 at the following positions:

Stn. 12, depth 2076 m; 56° 49'N:10° 15'W

Stn. 15, depth 1632 m; 56° 44'N:09° 28'W

Stn. 18, depth 1392 m; 56° 44'N:09° 20'W

Stn. 20, depth 1271 m; 56° 46'N:09° 17'W.

## COMMUNICATIONS

### **Omni glypta** sp. nov.

During the same month, and at roughly the same positions, specimens with small (<8 mm) slender annulated shells were taken at the following positions:

Stn. 14, depth 1770 m; 56° 45'N:09° 46'W

Stn. 15, depth 1632 m; 56° 44'N:09° 28'W.

Originally these were referred to the annulated fossil genus *Plagioglypta*, but are better placed in Habe's genus *Omni glypta*, proposed for recent forms with more slender shells and finer annulations than those of *Plagioglypta*.

### **Polyschides** sp. nov.

With a length of 15 mm these cadulid scaphopods, with pronounced apical notches, are relatively large. Nickles (*Bull. Mus. natn. Hist. nat. Paris* **1** (1979) pp. 41–77) described a 5 mm species, *P. cuspidatus*, and reported Verrill's *P. spectabilis* from Senegal and Liberia, W. Africa. These Rockall Trough specimens have the dimensions of *P. spectabilis* but not the shape which is nearer to the smaller *P. cuspidatus*. *Polyschides* is more abundant and more widely distributed along the east American seaboard and, until 1979, unknown from the East Atlantic.

Rockall Trough specimens were dredged from June to September 1973 at the following positions:

Stn. 4, depth 1993 m; 56° 52'N:10° 01'W

Stn. 6, depth 2900 m; 55° 03'N:12° 29'W

Stn. 10, depth 2540 m; 56° 37'N:11° 04'W

Stn. 18, depth 1392 m; 56° 44'N:09° 20'W.

I am grateful to John Gage of S.M.B.A. for permission to report these interesting scaphopods.

C. P. PALMER

Paleontology Dept., British Museum (Natural History), Cromwell Road, London SW7 3BD

(Received, 19th April 1986)

## INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

### ITZN 59

The following Opinions have been published by the International Commission on Zoological Nomenclature in the *Bulletin of Zoological Nomenclature*, volume **42**, part 2 on 27 June 1985:

#### *Opinion No*

1306 (p. 146) *Ledella bushae* Warén, 1978 is the type of species of *Ledella* Verrill & Bush, 1897 (Mollusca, Bivalvia).

1315 (p. 165) *Eolis alderi* Cocks, 1852 is the type species of *Aeolidiella* Bergh, 1867 (Mollusca, Gastropoda).

R. V. MELVILLE, Secretary, ICZN

c/o British Museum (Natural History), Cromwell Road, London, SW7 5BD

(Received, 3rd July 1986)

## DISTRIBUTIONAL RECORDS OF LAND MOLLUSCS FROM SOUTHERN MOROCCO

The following species of land snails and slugs found in and to the south of Marrakech in November 1985 have apparently not been recorded in southern Morocco before. Identification of the Limacidae was confirmed by dissection.

*Hawaiiia minuscula* (Binney, 1840). Five examples were found under a dead palm leaf in the Majorelle Gardens, Marrakech. This appears to be the first record from Africa of this species, which is apparently native only in the Americas and north Pacific region.

*Lehmannia valentiana* (Férussac, 1823). Four adults were found under stones on the banks of a small stream by the side of the road, below a large area of crags of tufa, at the south end of the Gorges de Mouley Brahim, 5 km N.E. of Asne.

*Deroceras* (*Deroceras*) *laeve* (Müller, 1774). One was found under a dead palm leaf in the Majorelle Gardens,



Marrakech. It is also found sparsely in damp ditches and marshy areas on the banks of the river near and between the villages of Asquine and Arhbalou in the Vallée de l'Ourika.

*Deroceras (Agriolimax) reticulatum* (Müller, 1774). Very common under stones in ditches by the side of the road near the village of Arhbalou in the Vallée de l'Ourika.

A. NORRIS  
City Museum, Municipal Buildings,  
Leeds, LS1 3AA.  
(Received, 12th May 1986)

### *PALUDINELLA LITTORINA* LIVING ALONG THE FLEET, DORSET

During May 1986 the writer made a visit to the Fleet to record molluscs occurring at various levels of the shore along the Chesil side. From the high water mark where Seaward has recorded *Leucophytia bidentata*, *Phytia myosotis* and *Truncatella subcylindrica* (Conchologists' Newsletter no. 95 December 1985), a sample of the stones and associated sediment and *Zostera* debris was taken and placed in a tray at the writer's home and observed for a short period each day over the succeeding two weeks. On the fourth day two specimens of *Paludinella littorina* (Chiaje, 1828) were observed crawling over the surface of stones within 2 to 3 cms of each other. No other specimens were subsequently found in this sample. The writer's identification has been confirmed by Dr Vera Fretter.

The species has a long history at this site (summarised in Seaward, *Proc. Dorset NHAS* (1978) C: 103), but there are no live records since 1888 for this locality (Sykes (1890) *J. Conch.* **6**, p. 166). Marshall (*J. Conch.* **14**, p. 67) gives a few sites in Cornwall and Devon and one in the Channel Islands; all before 1913. Seaward has been finding fresh dead shells of this species along the Fleet since September 1985 (*Porcupine Newsletter* (1986) **3** (6)), but the above live record represents a satisfactory rediscovery of this rare and local animal.

The site is an SSSI and the *Paludinella* colony is probably small since it is apparently restricted to an unusual interstitial habitat. Seaward informs me that specimens should not be collected without permission from the landowners and the NCC. The species is, however, very small and easily overlooked and may be present in similar sites along the Channel coast.

I am grateful to Dr Fretter for her help in confirming identification and to Dr Michael Kerney and Dennis Seaward for their information and advice.

JAN LIGHT  
88 Peperharow Road, Godalming, Surrey, GU7 2PN  
(Received, 1 July 1986)

## REVIEW

*North Atlantic Nudibranchs (Mollusca) seen by Henning Lemche*, by Hanne Just and Malcolm Edmunds, September 1985, Ophelia Publications, Marine Biological Laboratory, Helsingør, Denmark, 69 plates, 170 pp, £26.00 (soft covers), 25.7×17.4 cm.

Henning Lemche was an enthusiastic student of opisthobranch molluscs. Visitors to his house who were not interested in this topic might soon become bored, because all conversational roads soon led Lemche back into his favourite subject. I found him an excellent colleague, always willing to reply in detail and without delay to any request for help from a fellow enthusiast. In his own work on the taxonomy and biogeography of opisthobranchs he was extraordinarily meticulous and dedicated to the highest standards of scientific endeavour. This perfectionism was largely responsible for the painful fact that his life's work was uncompleted when he died in 1977. This was to have been a monograph, illustrated by his own water colour paintings, on the opisthobranch molluscs of northern Europe. There is some evidence that he had already decided to lower his sights, in the sense that he had recognised that he must concentrate his aim solely upon the smaller nudibranch group.

He left behind him a quantity of specimens together with colour slides and annotated drawings and paintings. Although the notes were, in the words of the authors 'often quite difficult to interpret', it was decided that the collections would 'constitute a most valuable base for further studies'. The primary need was for a co-ordinating author who could read Lemche's Danish notes (H. Just), and it would appear that the other authors (Dr M. Edmunds and Mrs E. Platts) were drawn into the project somewhat later. The now-published compendium appears under the names of Just and Edmunds, which might be thought to be unfair to Platts, who has contributed around 15 pages which represent a substantial portion of the text material; furthermore, the Platts section of the book, taking the form of an appendix entitled 'An annotated list of the north Atlantic Opisthobranchia', is of great usefulness to students of the group.

The body of this oddly shaped book (it resists all attempts to find a shelf in my study which will take it) consists of 69 colour plates which render Lemche's originals in a convincing fashion. Many of them are very good, for example, the representations of *Colga pacifica*, *Polycera faeroensis*, *Okenia aspersa*, *Diaphorodoris luteocincta* and *Flabellina borealis*. Some are not so good, as in the cases of *Flabellina verrucosa* (which in plate 44 is obviously abnormal, possibly dying, as the authors admit), *Tritonia nilsodhneri* (which is rarely if at all as pale as shown in plate 1), and '*Doto onusta*' (plate 11) which is probably *Doto coronata*.

There are two serious criticisms that must be levelled at this publication. Both are provoked by the fact that in my opinion the authors have produced a book which genuflects more to art than to science. This is expressed in the acknowledgements section, where thanks are rendered to the music of Ludwig van Beethoven for inspiration received, and in three separate aspects of the presentation. First, the selection of species for inclusion has been governed more by whether a suitable illustration could be found than by a desire for zoogeographic consistency. Despite the book's title 'North Atlantic Nudibranchs . . . .', specimens from the Friday Harbor Laboratories off the American north Pacific coast are the basis for plates 16, 34, 52, and 54.

My second criticism is that the authors have missed a real chance to make progress in the way that Lemche himself would surely have desired. Many times when reading this book, I felt that more anatomical observations were not only necessary but perfectly feasible. Lemche's collections are still there, are they not? So why did the authors stop short of investigating at the least the radulae of some of their unknowns? It is feeble for them to write (p. 5) that many of the specimens are 'still intact and available for examination in the future by specialists'. Edmunds and Just *are* specialists; whom else should we look to?

Thirdly, we expect better of the authors than their decision to include large numbers of species in the form of (for example) *Dendronotus* sp. A and B, *Adalaria* spp. A–C, and even Onchidorididae spp. A and B. Because the authors did not examine the anatomical features, they cannot identify these animals nor can they establish new taxa for them. The judgement to include them must have been primarily an aesthetic one. Such a reversion to an essentially pre-Linnean system of nomenclature cannot be welcomed. Lemche himself would surely have disapproved, as a commissioner of the ICZN. Such non-Linnean names are almost as bad as the colloquial names invented by some north American specialists, epitomised by the 'Jolly Green Giant' and 'Earthwatch Nudibranch' employed by Bartsch & Johnson in their book *Hawaiian Nudibranchs* (Oriental Publishing Company, 1981).

T. E. THOMPSON



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The Park, Cheltenham, Gloucester GL50 2RH

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# THE TERTIARY-RECENT BIVALVE *NOETIELLA* (ARCACEA) AND ITS EVOLUTIONARY RELATIONSHIPS

P. GRAHAM OLIVER<sup>1</sup>

(Accepted for publication, 19th April 1986)



**Abstract:** The arcoid genus *Noetiella* is defined to include small, non umbonate trapezoidal taxa possessing a prosodetic ligament and simple radial costae. Two subgenera are described; *N.* (*Noetiella*) – Pliocene to Recent and *N.* (*Scalenonoetia*) subg. nov. – Eocene. *N.* (*Noetiella*) contains three species; *N.* (*N.*) *congoensis* Thiele and Jaeckel, *N.* (*N.*) *minor* (Pallary) comb. nov. and *N.* (*N.*) *tethyensis* sp. nov. *N.* (*Scalenonoetia*) contains a single species *N.* (*S.*) *africana* (Newton). The anatomy of *N. congoensis* is described and reflects the infaunal habits in the form of the foot, musculature, lack of byssus and large palp size. *Noetiella* is compared with other infaunal noetids and shown to differ significantly from *Noetia*, *Eontia*, *Verilarca*, *Trinacria*, *Linter* and *Pachecoa*. The traditional subfamily trichotomy of Noetiinae, Striarcinae and Trinacriinae is questioned. The affinity of *Noetiella* is discussed on an individual lineage basis and is believed to belong to a distinct lineage separate from that of *Noetia*. A late Cretaceous ancestor is hypothesised which most probably resembled some of the more trapezoidal forms of *Breviarca*.

## INTRODUCTION

In a paper on the Recent Striarcinae of Hong Kong (Oliver 1985) I discussed specimens referred to as *Striarca afra* (Gmelin). Among the West African fauna three species have been consistently confused, namely *Striarca lactea* (L.), *Acropsis afra* (Gmelin) and *Noetiella congoensis* Thiele and Jaeckel. Moreover the systematic relationships of *Noetiella* are also confused, with this genus having been placed in the Trinacriinae (Reinhart 1935), Striarcinae (MacNeil 1938) and the Noetiinae (Newell 1969). I found (Oliver 1985) that similar confusions within the Striarcinae were the result of a lack of interpretation of shell morphology especially where the extremes of epibyssate and endobyssate characters were lacking. The Noetiidae have a primarily paleontological basis to their systematics and accordingly anatomical and functional data have not been widely employed. In this paper the anatomy of *Noetiella congoensis* is described and the functional morphology of the shell is interpreted from these data. From this base the paleontological data is re-examined and the evolutionary relationships of *Noetiella* are reconsidered.

Stanley (1972) in examining the evolution of endobyssate and epibyssate trends in the Arcoida noted how little was known of the Noetiidae. Thomas (1976) was equally speculative about the origin of the noetid ligament. Oliver (1985) and this paper are part of continuing studies on the noetids intended to elucidate their origins and subsequent radiation.

## GENUS *NOETIELLA* THIELE AND JAECKEL, 1931

Subgenus ***Noetiella* (*Noetiella*)** Thiele and Jaeckel, 1931

Type species: *Noetiella congoensis* Thiele and Jaeckel, 1931

<sup>1</sup> Sub-department of Invertebrate Zoology, National Museum of Wales, Cathays Park, Cardiff CF1 3NP



**Diagnosis:** Small shells: equivalve; inequilateral, expanded anteriorly, somewhat truncated posteriorly, outline trapezoidal, anterior margin rounded, posterior margin straight. No byssus gape or median sinuation; Moderately inflated; Dorsal area moderately long, proportionately moderately wide, umbos not particularly prominent, orthogyre – slightly opisthogyre; Ligament covering most of the dorsal area, prosodetic or secondarily amphidetic. Sculpture primarily radial, of numerous low costae or riblets, concentric sculpture of numerous fine lines; Periostracum thick, scaly; Hinge moderately developed, teeth in two barely separated series increasing in size laterally. Adductor scars unequal, the anterior slightly larger, the posterior with a low myophoric ridge; Inner margin fluted.

**Distribution:** West Africa, Southern Europe, Arabian Gulf (Pliocene to Recent).

**Noetiella (Noetiella) congoensis** Thiele and Jaeckel, 1931

(Pl. 24, Figs. 1, 2)

*N. congoensis* Thiele and Jaeckel, 1931, p. 176, Pl. 6, fig. 11.

*A. lactea* Dautzenberg, 1912, p. 86; (pars).

*A. lactea* Nicklès, 1955, p. 116; (pars).

*A. afra* Dell, 1964, p. 237.

**Syntypes:** Humboldt Museum; Berlin.

**Other Material examined:** 15 valves, 4 miles SW of Conakry, Senegal, NMW.1955.158.; Abidjan, Ivory Coast MHNP:— 1 spec. 42 m; 2 spec. 30 m; 2 spec. 30 m; 5 spec. 60 m; 1 spec. 25 m; 1 spec. 80 m; 2 spec. 40 m; 3 spec. 60 m; 10 spec. 60 m; 1 spec. 40 m; Sassandra, Ivory Coast MHNP: — 1 spec. 50 m; 1 spec. 30 m; 1 valve Angola, Discovery Stn. BM(NH): 5 valves, Ilha de Luanda, 90 m, MHNP: Senegal – Angola, Atlantide Expedition, ZMC: 2 v., St. 54, 6°05'N, 10°25'W, 22–25 m.; 2 v., St. 55, 6°03'N, 10°25'W, 44 m.; 1 spec. and 1 v., St. 56, 6°01'N, 10°26'W, 50–55 m.; 1 v., St. 66, 4°27'N, 7°07'W, 66 m. 1 v., St. 68, 4°38'N, 6°18'W, 80–90 m. 1 v., St. 70, 4°50'N, 2°49'W, 60–65 m.; 1 spec and 1 v., St. 72, 4°51'N, 1°42'W, 24 m.; 1 v., St. 85, 5°37'N, 0°38'E, 50 m.; 1 v., St. 101, 5°59'N, 4°36'E, 17 m.; 1 v., St. 129, 6°15'S, 13°20'E, 12 m.; 6 v., St. 141, au large de Freetown, 15 m.; 1 v., St. 145, 9°20'N, 14°15'W, 32 m.; 6 v., St. 156, au large de Bathurst, 18 m.

**Shell morphology.** Shell small, trapezoidal with up to 60 low radiating riblets, crossed by numerous fine concentric lines giving minute ridges on the radiating riblets. Occasional bifurcation of the riblets on the median-posterior junction. Ligament prosodetic but slightly amphidetic in large individuals (Figs. 10a–c). Periostracum persistent, rusty brown in colour, scaly except posteriorly where minute blunt lamellar hairs arise from the riblets. Muscle scars well defined with slight myophoric ridges, inner margin evenly fluted.

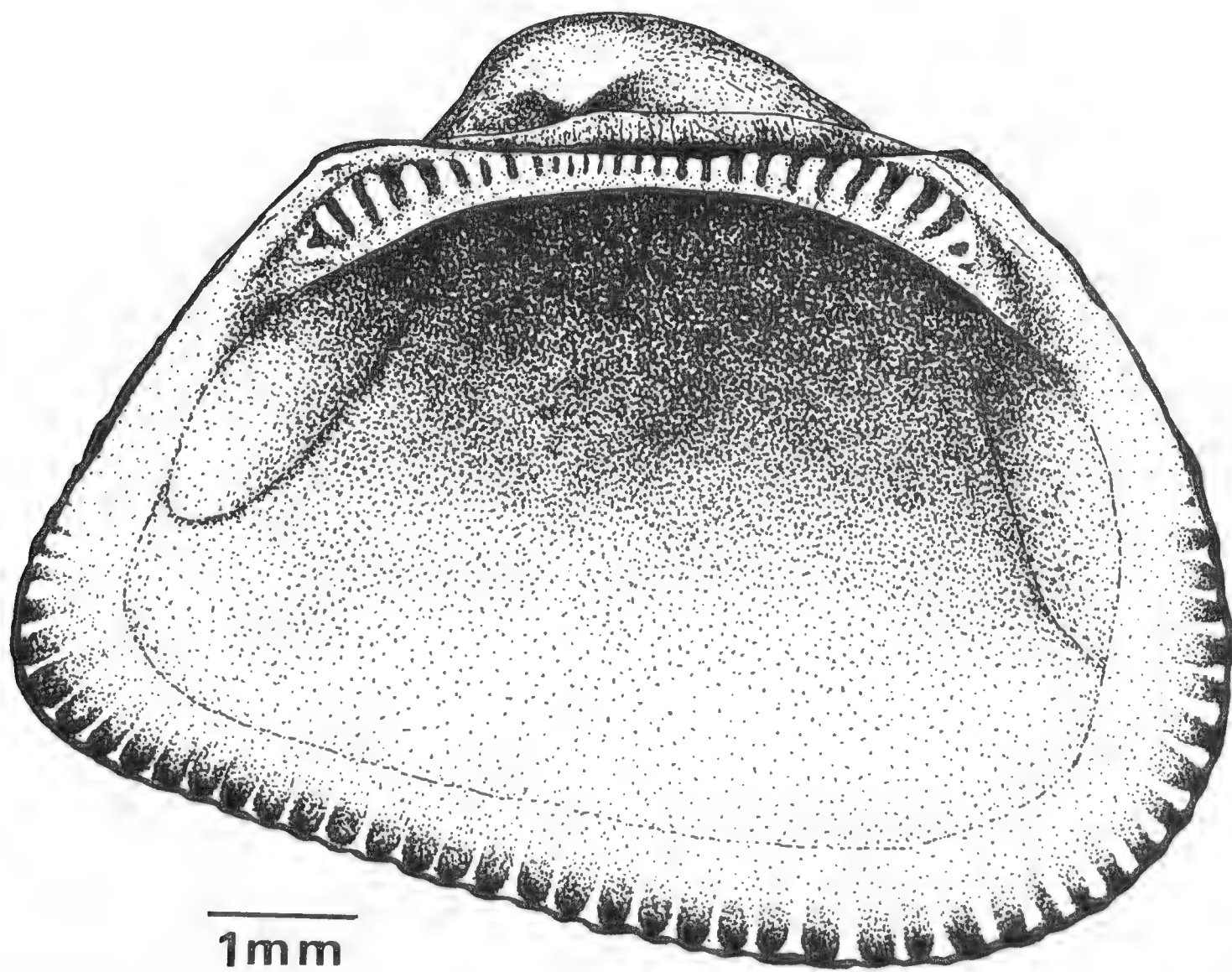
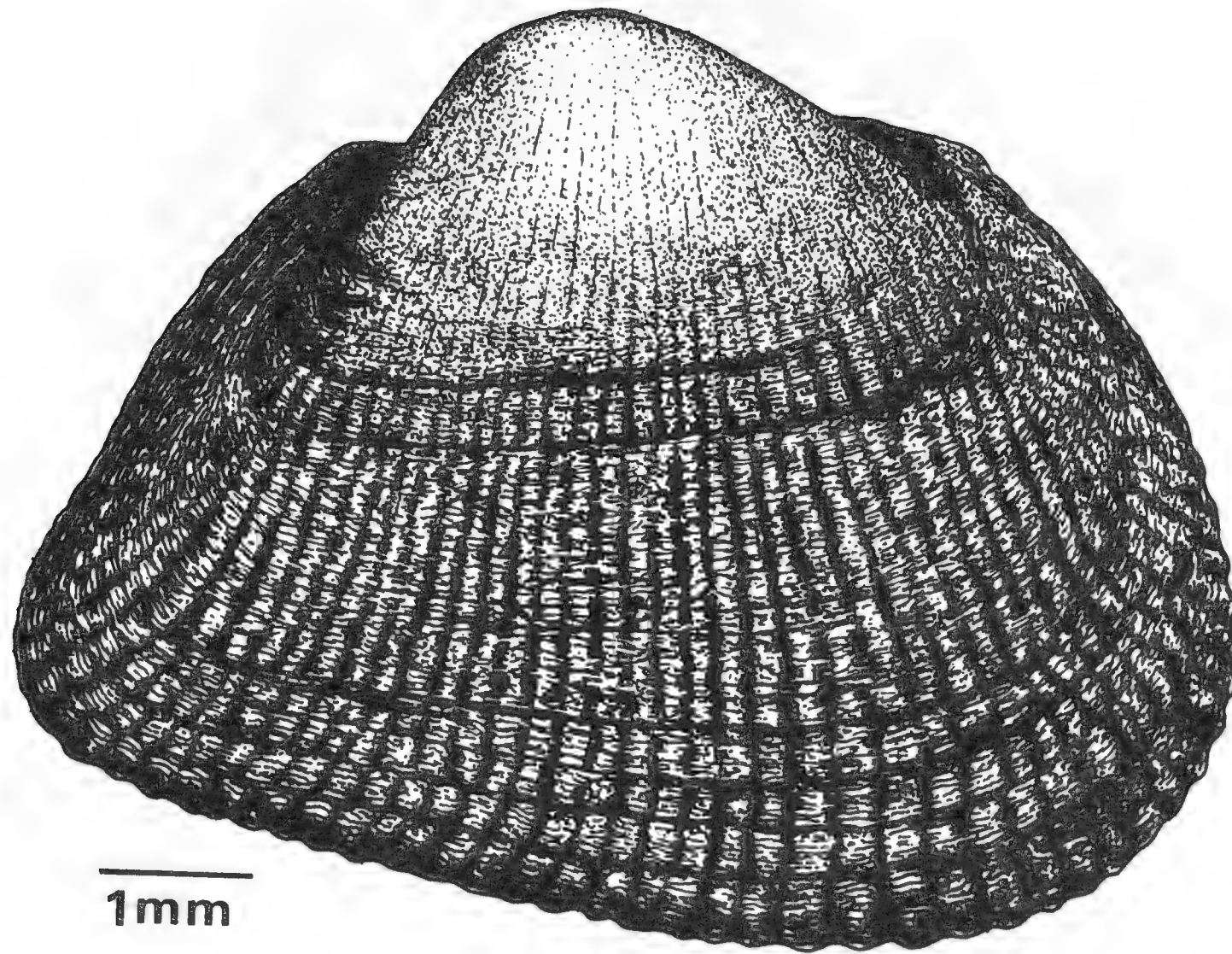
**Mantle** (Fig. 4): The mantle is opaque, thick. The mantle edge is simple along the ventral and posterior margins but bears small folds anteriorly and well developed folds at the posterior ventral angle. These posterior folds indicate that discreet inhalent and exhalent apertures can be formed.

**Ctenidia and labial palps** (Fig. 4): The ctenidial structure is typical of other arcoids and is homorhabdic, nonplicate and filibranch. The inner demibranch is slightly larger than the outer. The labial palps possess thirty ridges. There is a narrow non-ridged oral fold.

**Abdominal region** (Fig. 5): The abdominal organs are small and ovoid, gladular pads overlying the visceral ganglion are present but are undifferentiated from the surrounding epithelium.

**Foot and musculature** (Fig. 4): The foot is large with a large toe and small heel. The toe is deep and compressed. A ventral groove is present but no byssus was observed. The pedal retractors are subequal, the posterior ones slightly larger, the anterior protractors are well developed attaching along a broad area ventral to the anterior adductor.

**Alimentary canal** (Fig. 4). The oesophagus is flattened dorso-ventrally, short and enters the stomach high on the anterior face. The combined style sac and mid gut leaves the stomach ventrally and then passes sharply forward turning on itself and then curving dorsally



Figs. 1–3. *Noetiella congoensis*: Ivory Coast MHNP, Fig. 1 exterior of right valve, Fig. 2 interior of left valve, Fig. 3 (overleaf) dorsal view.

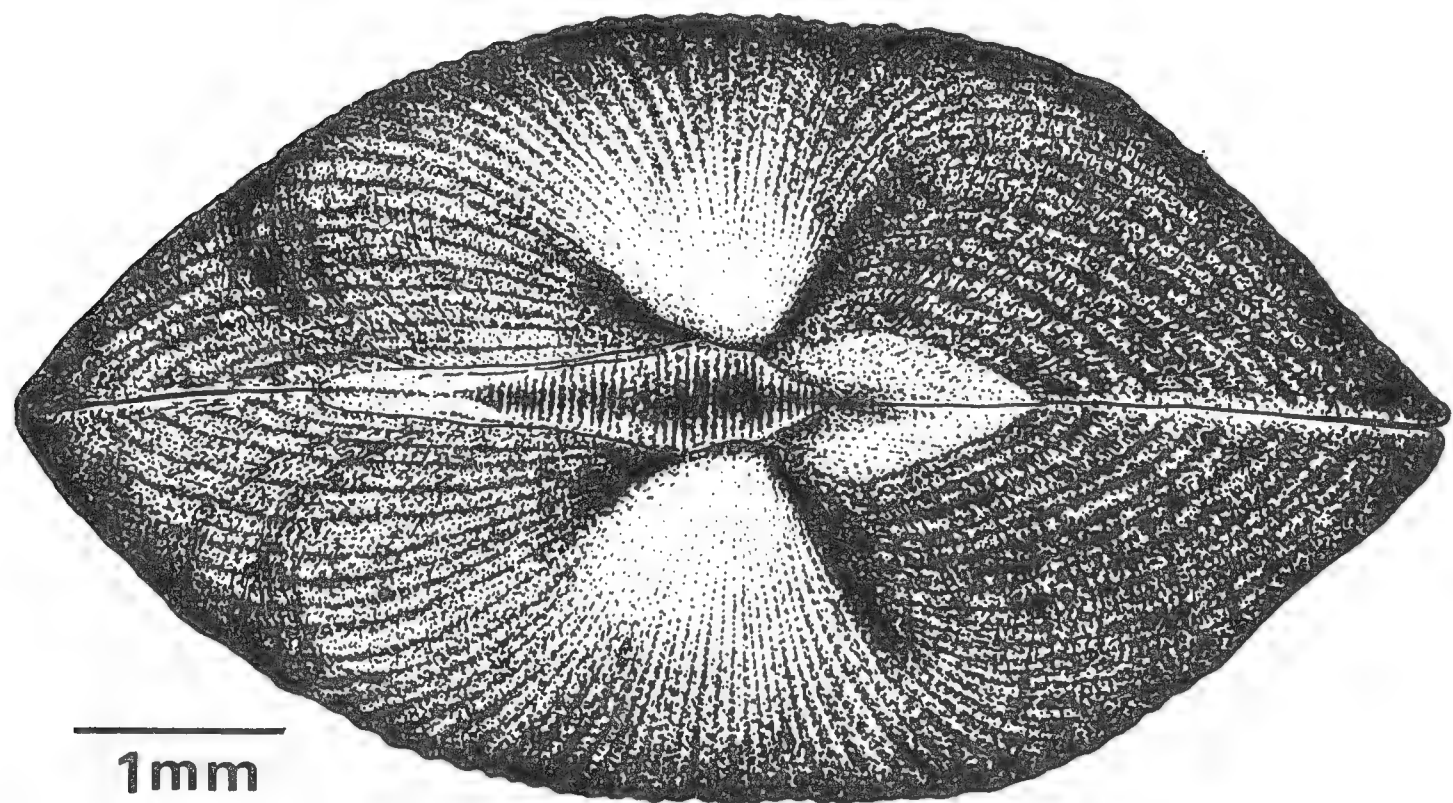


Fig. 3. *Noetiella congoensis*: Ivory Coast MHNP, dorsal view.

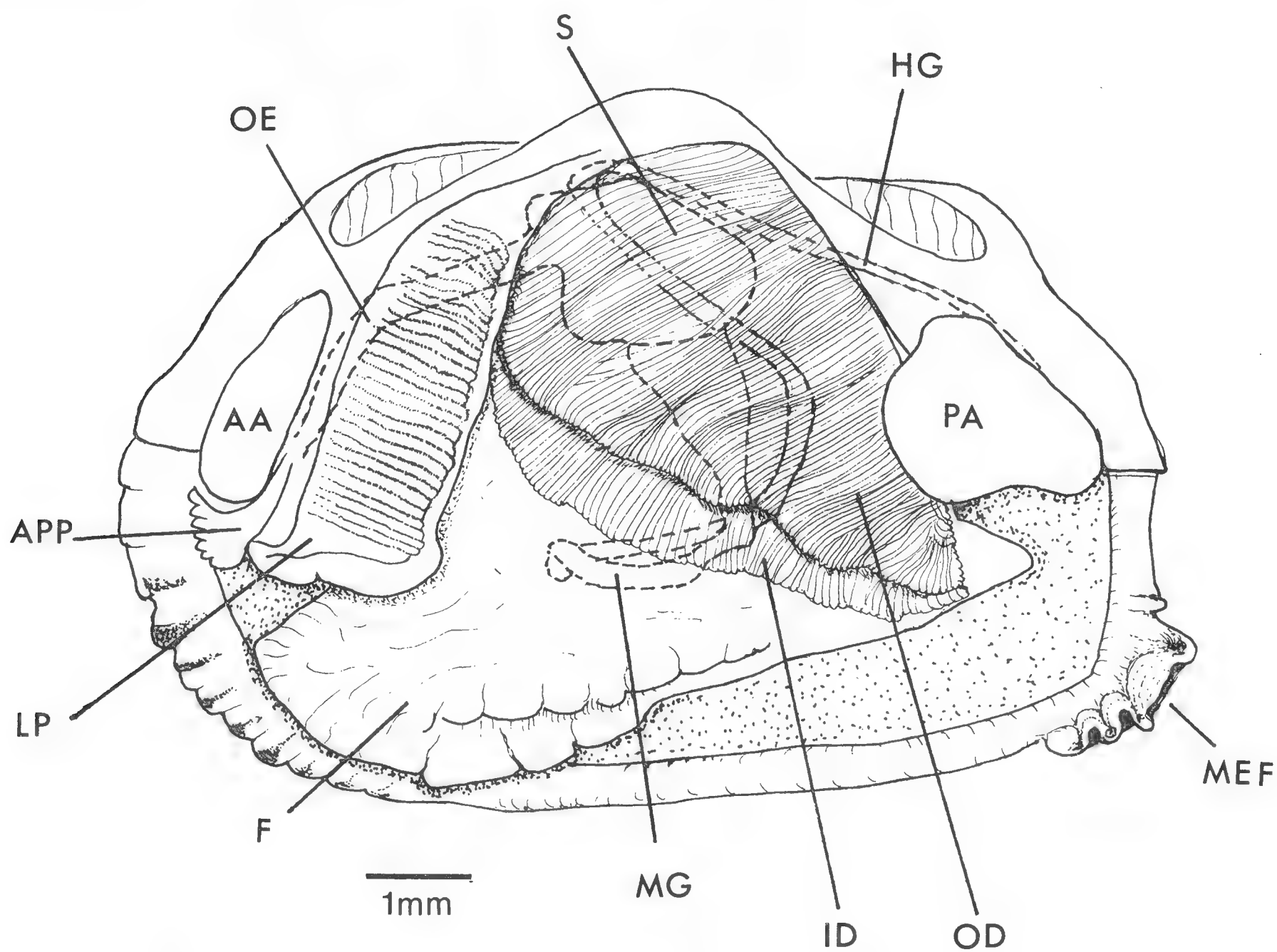


Fig. 4. *Noetiella congoensis*: Gross anatomy viewed from the left side after removal of mantle and ctenidium.

*Key to abbreviations used in anatomical diagrams*

A anus, AA anterior adductor, APP anterior pedal protractor, DDD ducts to digestive diverticula, DH dorsal hood, F foot, FSC food sorting caecum, GA gill axis, GT glandular tissue, HG hind gut, ID inner demibranch, LP labial palp, MEF mantle edge folds, MG mid gut, OD outer demibranch, OE oesophagus, PA posterior adductor, RDT right dorsal tract, RVT right ventral tract, S stomach, SS style sac, VG visceral ganglion.



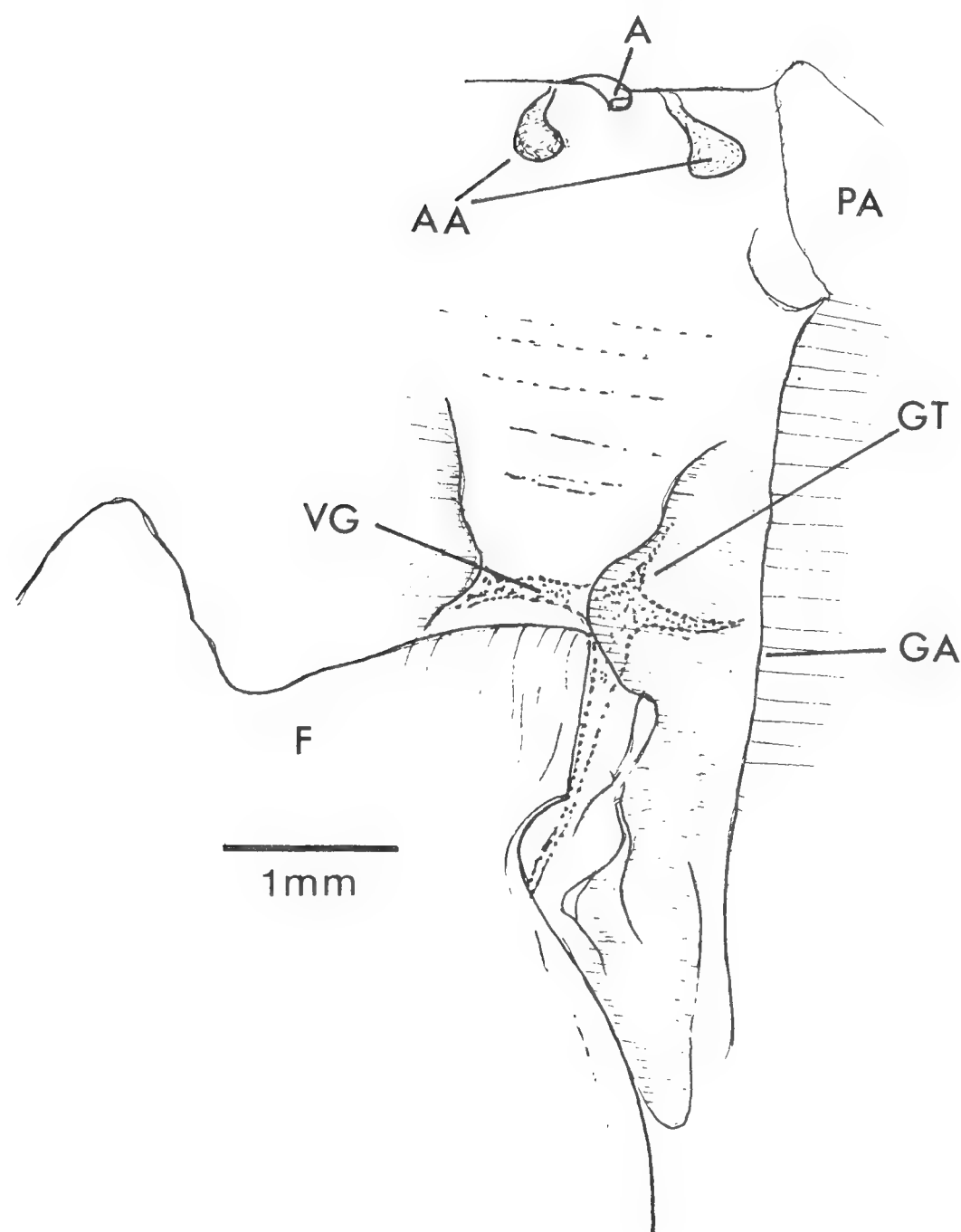
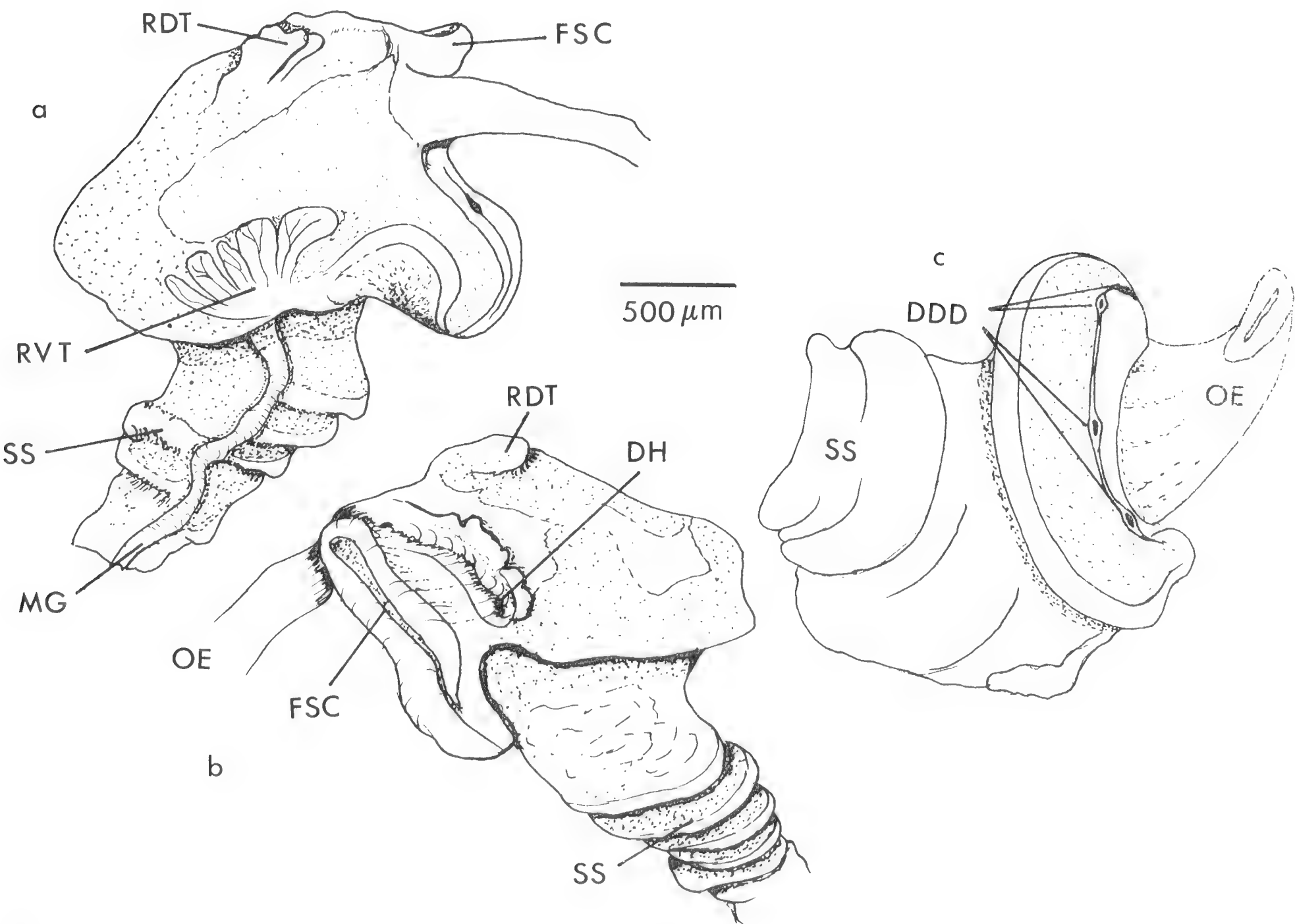


Fig. 5. *Noetiella congoensis*: The abdominal region.



Figs. 6a–c. *Noetiella congoensis*: The stomach (a) right side, (b) left side, (c) ventral.



passing well across the right side of the stomach before turning again posteriorly to form the hind gut. The stomach (Figs. 6a–c) displays well differentiated features. The food sorting caecum is well developed as a circum oesophageal groove, running ventrally and posterior to it is the groove containing the four digestive diverticula ducts. There is a deep hood tract and dorsal hood forming a prominent protrusion across the left dorsal area. There is a prominent right dorsal protrusion marking a second sorting pouch. On the right ventral side is a very prominent region of thick folds which display a peculiar venation pattern. The rejection tract can be seen leaving this region and running down the right side of the combined style sac and mid gut. The style sac is extraordinarily strongly ridged.

*Comparisons:* Although confused with *Striarca lactea* and *Arcopsis afra*, (Dautzenberg 1912, Nickles 1955) *N. congoensis* differs greatly in sculpture and outline. Both *S. lactea* and *A. afra* are barbatiform, unlike the anadariiform *N. congoensis*. The sculpture of *S. lactea* and *A. afra* is much coarser, radially ribbed or decussate. The periostracum of *N. congoensis* is scaly unlike the filamentous bristles of *Striarca*. Both *S. lactea* and *A. afra* are epibyssate nestling forms unlike the free living burrowing *Noetiella*.

*Remarks:* The general anatomy of *Noetiella* is typical of burrowing arcoids, notably the form of the foot with the deep toe, the well demarcated mantle edge and the relatively large palps. In these respects *Noetiella* resembles *Verilarca* (Oliver 1985). The stomach is unusual in the development of the internal structures especially the right ventral tract, right dorsal depression and style sac ridges. This would indicate a high degree of sorting and very active crystalline style. Heath (1941) noted a complex stomach structure in *Noetia* and a comparison with his figures reveal strong similarities although the right side is poorly described.

**Noetiella (Noetiella) minor** (Pallary, 1939) new comb.

(Pl. 24, figs. 3, 4)

*Arca pectunculiformis* var *minor* Pallary, 1939, pp. 125–126, Fig. 14.

Lectotype (here chosen) BM(NH) 1934.11.15.136., Arbat Creek, Basra, ex MacFadyen Coll. subfossil. Other material examined: Paralectotypes as lectotype (BM(NH) 1934.11.15.137–141; 2 spec. Arbat Creek, Basra, ex Melvill-Tomlin coll. NMW.1955.158. subfossil; 1 spec., Aljanin, Kuwait ex. Smythe coll. live collected; 8 spec. Persian Gulf. BM(NH) 1893.12.15.25–32; 47 valves, Basra and Mohamera ex W. K. Loftus BM(NH) Geol. Dept. L27063–4.

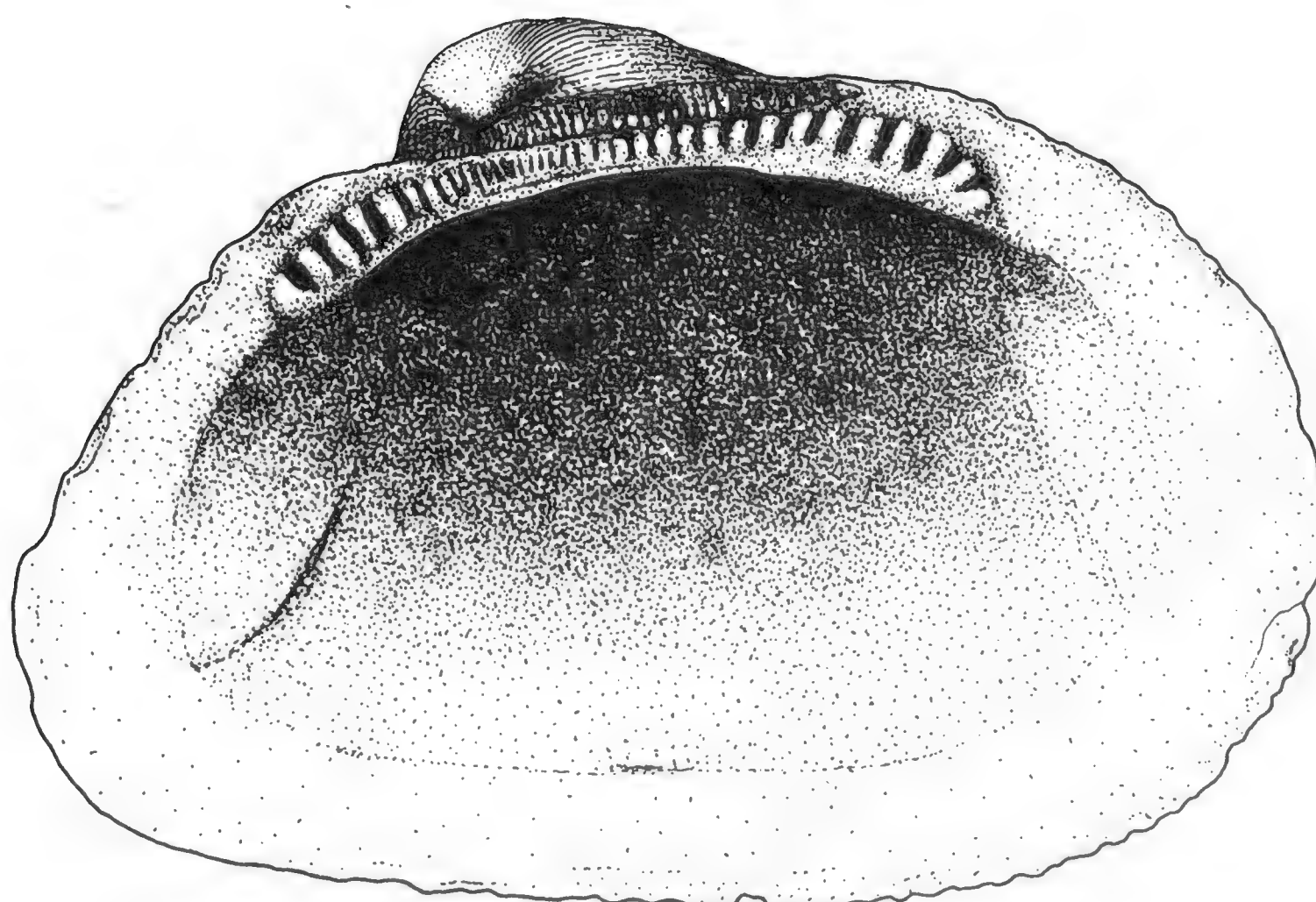
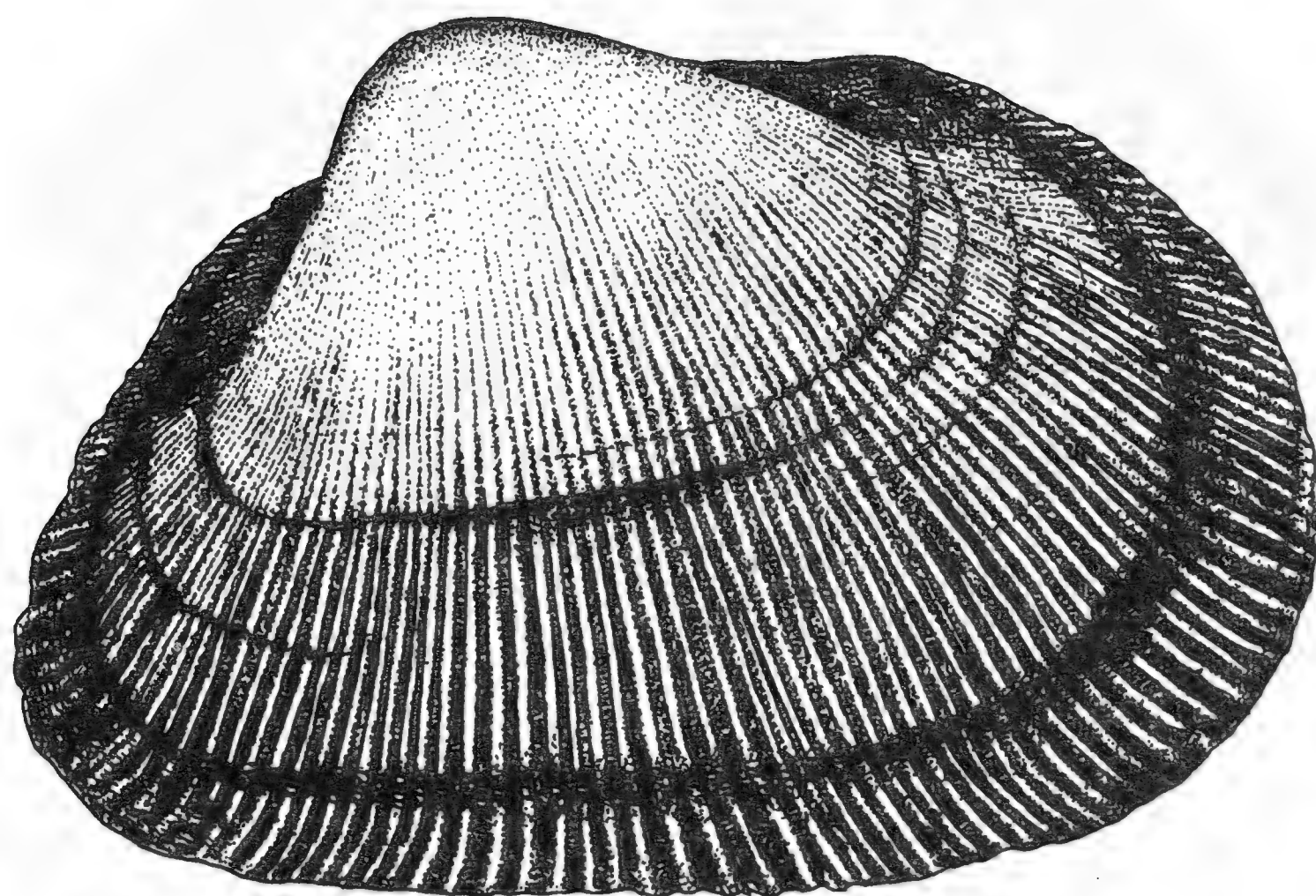
*Description:* Shell small, equivale roundly trapezoidal, expanded anteriorly with rounded anterior margins, partially truncate posteriorly, umbos opithsogyre, dorsal area narrow, ligament prosodetic. Sculpture of 91–98 radial riblets alternating strong and weak over the median area, crossed by numerous concentric lines which give rise to minute ridges on the riblets. Periostracum scaly but poorly retained. Hinge teeth in two poorly separated series, the anterior set slightly smaller. Inner margin weakly fluted.

*Remarks:* Although originally described as a variety of '*Barbatia*' *pectunculiformis*, Dunker the two species are quite different. '*B.*' *pectunculiformis* is almost equilateral, has an amphidetic ligament and has a much weaker sculpture of many more radial raised striae.

*Dimensions:*

	<i>Length</i>	<i>Height</i>	<i>Tumidity</i>
Lectotype:	15.9	11.5	8.4
Paralectotypes: Basra	16.45	11.2	8.2
	13.9	10.05	8.7
	10.65	7.6	5.6
	14.2	10.2	6.1
	13.1	9.5	3.6
	13.6	10.5	7.6
	11.8	8.7	6.4
ex. Smythe coll.: Kuwait	16.1	11.9	9.4

*Distribution:* Persian Gulf only – Recent.



Figs. 7–9. *Noetiella minor*: Kuwait, Smythe Coll. Fig. 7 exterior of right valve, Fig. 8 interior of left valve, Fig. 9 (overleaf) dorsal view.

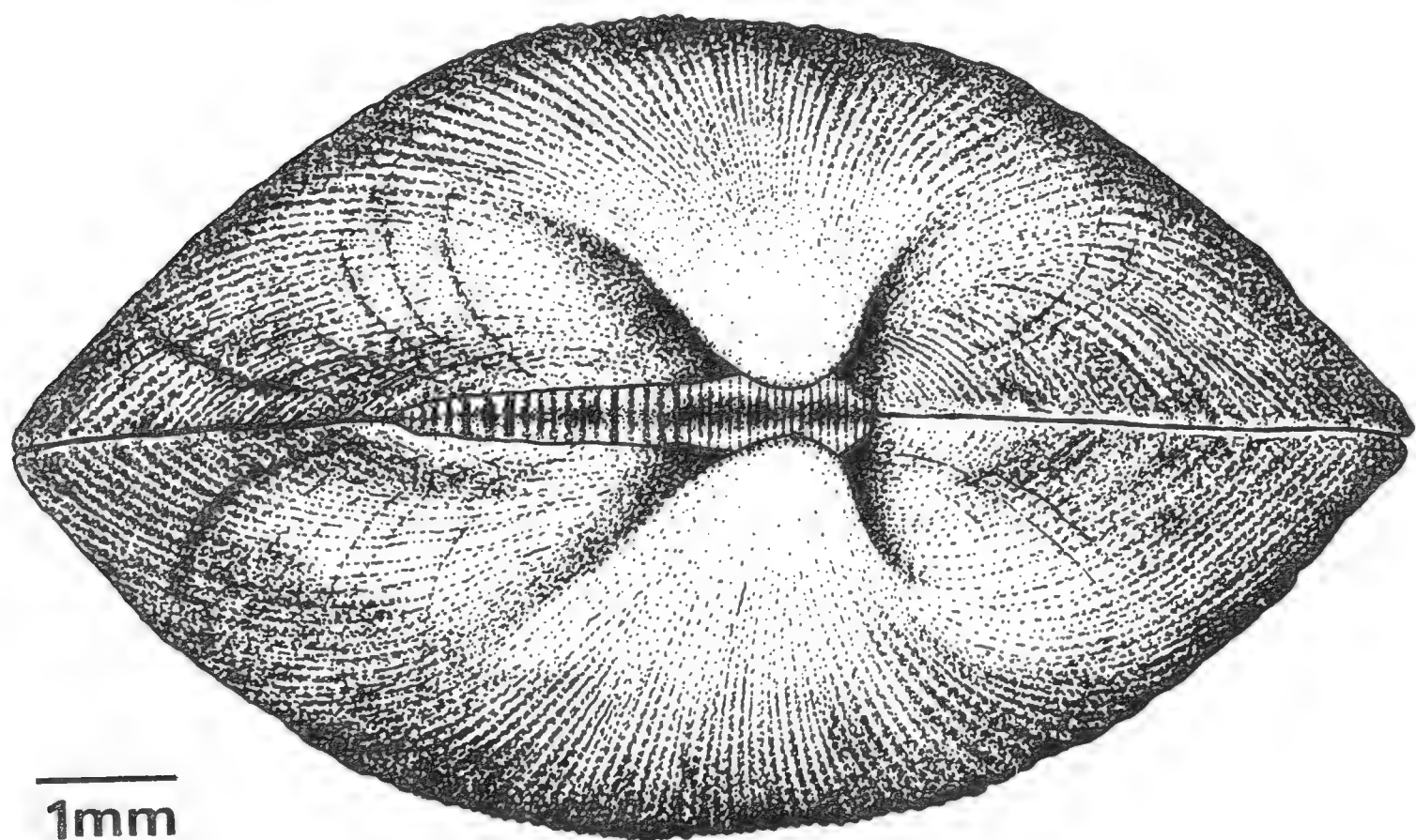


Fig. 9. *Noetiella minor*: Kuwait, Smythe coll, dorsal view.

**Noetiella (Noetiella) tethyensis** sp. nov.

(Pl. 24, figs. 5, 6, 7)

*Holotype*: BM(NH) Geol. Dept. LL40801. N.W. bank of the Arno, Valle Maggiore, Tuscany, Italy from clay under *Cardium hians* bed., Pliocene.

*Paratypes*: 2 spec. as holotype LL30104, LL30091; 2 spec. same locality in *Potamides* bed. BM(NH) Geol. Dept. LL30083, LL30074. All specimens ex Coll. W. Heap.

*Dimensions*:

	<i>Length</i>	<i>Height</i>	<i>Tumidity/ Single valve</i>
Holotype	12.7	9.1	4.1
Paratypes	10.1	7.3	2.85
	8.4	5.5	2.2
	8.95	6.05	2.55
	8.20	5.55	2.45

*Description*: Shell small, equivalve, roundly trapezoidal, considerably expanded anteriorly, with rounded anterior margin, truncate posteriorly, with straight posterior margin, umbos slightly opisthogyre, dorsal area narrow, ligament prosodetic but secondarily amphidetic in large individuals (Figs. 11a–b). Sculpture of 69–98 riblets depending on size, especially in larger individuals where many fine riblets are present on the posterior truncated area. A few posterior median riblets may be bifid and there may be an occasional very fine interrib costa. Concentric sculpture of numerous lines best preserved between the riblets. Hinge teeth in two poorly separated series, the anterior set being slightly smaller. Inner margin strongly fluted. Muscle scars subequal with a very weak myophoric ridge on the posterior scar.

*Distribution*: Known only from the Upper Pliocene, Calabrian of Tuscany, Italy.

*Etymology*: After Tethys, the Mesozoic-Tertiary Ocean.

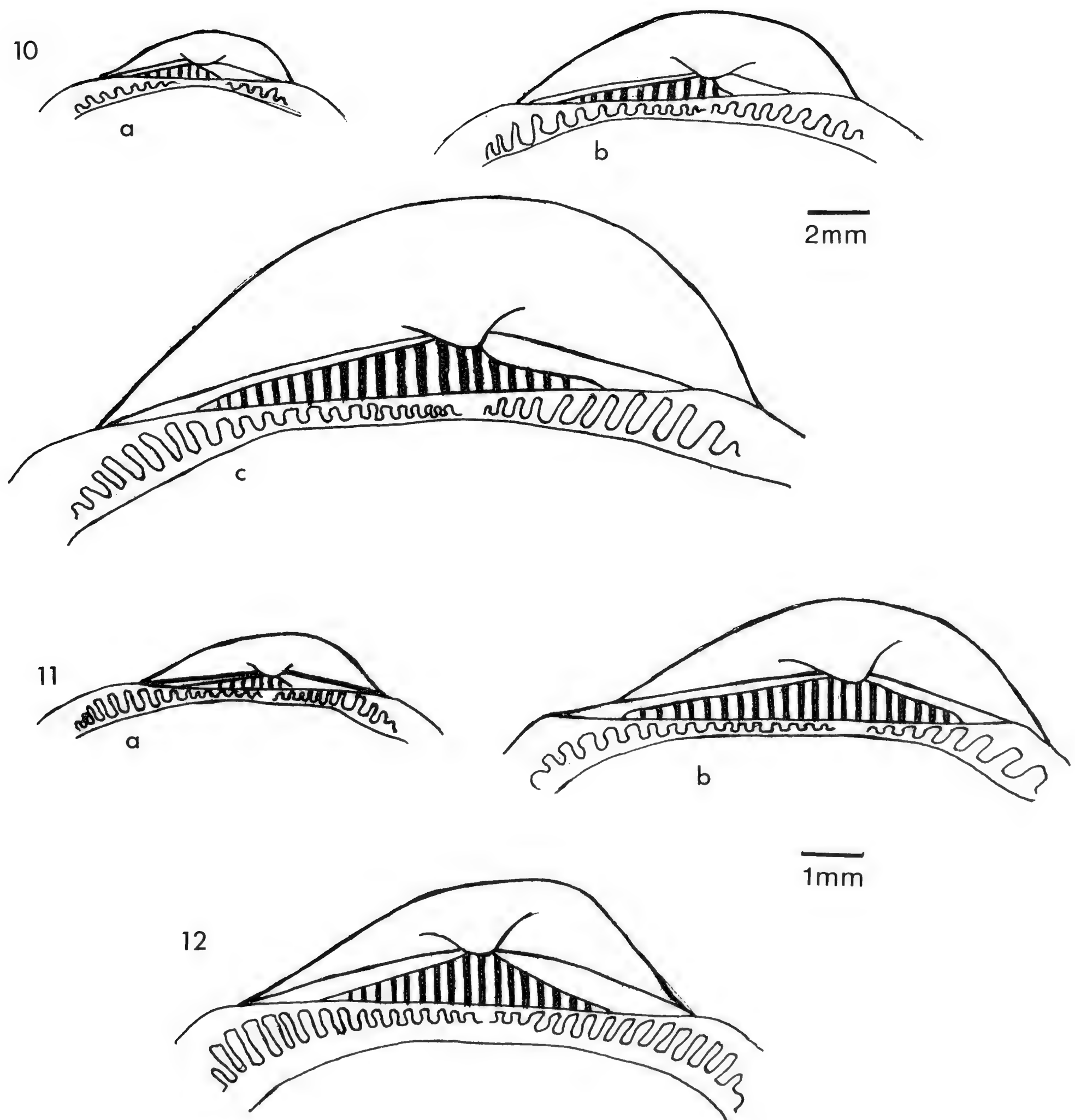
*Remarks*: This species has obvious affinity with *N. (N.) minor* (Pallary) but differs in the form of the radial sculpture and presence of internal crenulations.

**Noetiella (Scalenonoetia)** subgen. nov.

*Type species*: *Fossularca africana* Newton, 1922. Nigeria, (Eocene).

*Diagnosis*: As *Noetiella* (*Noetiella*) but more quadrate, less expanded anteriorly, inequivalve and with secondarily amphidetic ligament.





Figs. 10a–c. Ligament of *Noetiella congoensis*: ontogenetic series.

Figs. 11a–b. Ligament of *Noetiella tethyensis*: ontogenetic series.

Fig. 12. Ligament of *Scalenonoetia africana*.



*Distribution*: W. Africa only, Eocene.

*Etymology*: Scalen (Latin), unequal, referring to the inequivalve character.

**N. (Scalenonoetia) africana** (Newton, 1922), comb. nov.

(Pl. 25, figs. 1, 2, 3)

*Fossularca africana* Newton, 1922, p. 68–69, Pl. 8, figs. 14–17.

*Fossularca africana* Newton, 1957, Eames, p. 54.

*Material*: Type BM(NH) Paleontology, types and supplementary series all from Ameki, Southern Nigeria. Eocene. Lectotype L48113, Paralectotypes L48134–6, L48157–63, L48120–7, L48118–9, L48114–7, L48112, L48146–51, L48143–5, L48140–2, L48128, L48103–11. (Lectotypes selected by Eames (1957).

*Description*: Shell, heavy, slightly inequivalve with the left valve overlapping the right valve, inequilateral, trapezoidal with an expanded anterior area, anterior margin rounded, posterior margin straight, post-ventral junction strongly angulate. Dorsal area moderately wide, umbos slightly opisthogyre, ligament secondarily amphidetic (Fig. 12), but with a notable anterior displacement, sculpture of numerous radial costae crossed by fine concentric lines, the radial costae of the left valve fewer, more widely spaced and heavier anteriorly than those of the right valve. Hinge straight, with up to 40 teeth in a single series, inner margins crenulate.

*Remarks*: This species is very similar to the Recent *N. (N.) congoensis* but differs in its larger heavier inequivalve shell. The sculpture is stronger and the post-ventral junction more angulate. The ligament is apparently amphidetic but the larger posterior ligament area suggests that as in *N. tethyensis* this is a secondary condition derived from a primarily prosodetic ligament.

*N. (Scalenonoetia) africana* was first described as a *Fossularca* (= *Arcopsis*), but the form of this species is clearly infaunal and unlike the epifaunal *Arcopsis* or *Striarca*. *Scalenonoetia* although inequivalve is not uniquely so among the Noetiidae. The fauna of the Upper Cretaceous, Ripley Formation of Coon Creek, Tennessee contains two inequivalve species (Wade 1926).

*Breviarca saffordi* (Gabb) (Pl. 25, figs. 4, 5) (12 valves, BM(NH) Geol. Dept., examined) resembles other small infaunal noetiids in that the anterior area is slightly expanded with rounded margins, the posterior is truncate with a gently curved posterior margin. There is no byssal notch or median sinus. It differs from *N. (Noetiella)* and *N. (Scalenonoetia)* in the ligament which is truly amphidetic and in sculpture which is primarily concentric with very weak closely spaced radial striae. The inequivalve condition is marked, the left valve having a deep submarginal groove into which the right valve fits. Wade (1926) did not mention the inequivalve condition and presumably Newell (1969) was unaware of it when he synonymised *Breviarca* with *Striarca*.

The second species was described by Wade (1926) as *Limopsis perbrevis* (Pl. 25, figs. 6, 7) but the ligament is distinctly striate vertically and set in an incised triangular area which cannot be described as a resilifer. The ligament does not interrupt the hinge as in *Arcopsis* or *Trinacria*. In outline this species resembled a contracted *Noetiella* but is almost as high as long and is very tumid. The ligament is small and truly amphidetic and the sculpture is weak with radial striae marginally stronger than the concentric lines. In these characters this species differs from *Scalenonoetia* as in *B. saffordi* the left valve has a strong submarginal groove. This is not the place to discuss the generic status of *perbrevis* but it can be referred to *Breviarca* for the present based on the similarities in general form, ligament and weak sculpture.

In rejecting the synonymy of *Breviarca* with *N. (Scalenonoetia)*, I place greater emphasis on the ligament condition rather than the inequivalve character. Outgroup comparison within the Arciidae suggests that the inequivalve condition is homoplasous and is shared by such

different genera as *Cunearca* and *Bathyarca*. Oliver and Allen (1980) showed that *Bathyarca* was unique among the Arciidae in possessing mantle flaps and therefore a monophyletic group. Within *Bathyarca* the inequivalve condition is strongest in those species which are infaunal.

## DISCUSSION

### *Noetiella* as a generic concept.

From anatomical observations on *N. (N.) congoensis* I conclude that *Noetiella* is an infaunal genus. As such it is comparable with *Noetia* and *Eontia* of the Noetiinae, *Verilarca* of the Striarcinae and by inference on shell characters with *Linter*, *Trinacria* and *Pachecoa* of the Trinacriinae. Stanley (1970) described the form and function of *Eontia ponderosa* showing it to be a poor burrower in unstable sandy sediments. The umbonate form and relatively massive shell are related to this habit. By contrast *Noetiella* lives in offshore muds and is not adapted to survive wave scour, in that the shell is not massive, the ribs are not prominent and the form is not umbonate. *Noetiella* furthermore does not possess dominant secondary ribbing as noted by MacNeil (1938). There is the possibility that the *Noetia/Eontia* ribbing is a consequence of overall size but this is not substantiated in other large arcaceans such as *Anadara* where the primary ribbing remains dominant throughout ontogeny. The functional and purely phenetic differences between *Noetia/Eontia* and *Noetiella* lead me to conclude that Newell's (1969) synonymy is unwarranted.

MacNeil (1938) referred *Noetiella* to the Striarcinae and within that subfamily there is a resemblance to the genus *Verilarca*. Like *Noetiella*, *Verilarca* is a inhabitant of offshore muds (Oliver 1985) and shares the functionally related characters of slight anterior expansion, a poorly defined posterior carina and an anatomy agreeing in the musculature, form of the foot and palp size. In contrast *Verilarca* possesses a truly amphidetic ligament and nodulose ribs.

The stomach features of *Noetiella* are more akin to *Noetia* in the complexity of the ridging of the right side and style sac. At this point I do not refute MacNeil's (1938) suggestion that *Noetiella* belongs to the Striarcinae but I would conclude that because of the differences detailed above *Noetiella* cannot be synonymised with the infaunal striarcinid genus *Verilarca*.

Reinhart (1935) linked *Noetiella* to *Halonanus* (Stewart 1930) a member of the Trinacriinae. In general shell form this is the case but as with other genera of the Trinacriinae (*Linter* and *Trinacria*), *Noetiella* does not share the feature of the ligament being set in a resilifer. For this reason I cannot synonymise *Noetiella* with any of the genera of the Trinacriinae.

*Noetiella* is therefore considered here as a useful generic grouping comprising four species, in two subgenera and having a Tethyan distribution from West Africa to the Arabian Gulf from Eocene to Recent.

### *Higher Taxa Affinities of Noetiella*

The Noetiidae are traditionally divided into three subfamilies; Noetiinae, Striarcinae and Trinacriinae. The systematic position of *Noetiella* has been disputed, MacNeil (1938) referring it to the Striarcinae and Newell (1969) to the Noetiinae. Resolution of this debate should be possible by comparing the shared derived characters of *Noetiella* to those of the three subfamilies, but this is not straightforward as the subfamilies themselves are not based on such criteria.

*Striarcinae*: Newell's definition includes 'small ovoid costellate forms with an amphidetic ligament'. Small ovoid forms also exist in the Noetiinae (*Didimacar*) and in the Trinacriinae

(*Pachecoa*). The amphidetic condition can be regarded as primitive with secondarily derived opisthodetic and prosodetic orientations, and as such is symplesiomorphic within the Noetiidae.

*Trinacriinae*: This subfamily is based primarily on the presence of a resilifer but this character is also shared by *Arcopsis* and *Trigonodesma* which are regarded as members of the Striarcinae. Ligament orientation is variable in the Trinacriinae, being opisthodetic to prosodetic. The weak radial sculpture is also shared by traditional members of the Striarcinae, namely *Estellacar*, *Rectangularca* and *Breviarca*.

*Noetiinae*: Newell's (1969) definition rests primarily on the form represented by *Noetia* and *Eontia*, i.e. the trigonal, inequilateral forms possessing opisthodetic to prosodetic ligaments, which normally have dominant secondary ribbing. I have examined *Noetia magnifica* in which I can find no trace of secondary ribbing. Also included, however, are genera such as *Didimacar* which resembles *Striarca* but with an opisthodetic ligament. The inclusion of this genus is presumably based on ligament orientation, however if all orientations can be present in the Noetiinae why not in the Striarcinae? Even within the trigonal forms there is evidence that two radiations have occurred (MacNeil 1938). *Eontia* appears to be derived from a semi-infaunal or epifaunal ancestor represented in the Lower Miocene by *E. incile*. This radiation is separate from the *Noetia* radiation which had already taken place by the Eocene. For the present I agree with MacNeil for Stanley (1970) shows the retention of a sheet byssus in *E. ponderosa*, a character which is most unusual in infaunal arcoids. A sheet byssus is commonly found in epifaunal arcoids and this suggests to me a relatively recent adoption of the infaunal habit.

All three subfamilies appear to be based primarily on the genera from which they take their names. In many cases the inclusion of other genera is based on the absence of characters or presence of symplesiomorphies and only rarely on synapomorphy. Indeed the apomorphic nature of characters such as the resilifer, prosodetic ligament and form of ribbing has never been considered. I prefer to abandon the current subfamily taxa in preference for smaller phyletic lineages.

The key character requiring assessment is the prosodetic ligament. *Noetiella* displays a prosodetic ligament in small individuals but a secondarily amphidetic condition appears in large individuals in which considerable inter-umbonal growth has occurred. This type of ligament growth is common to three middle Eocene taxa all from Nigeria: *N. (Scalenoneotia)* (this paper), *Protonoetia* (MacNeil 1937, Freneix 1959) and *Africarca* (Eames 1957, Freneix, 1959, Struogo 1979). Thomas (1978) illustrated how interumbonal growth weakens the strength of the arcoid ligament and how this is counteracted by inturning of the umbos. Thomas' findings therefore suggest that mechanisms for avoiding interumbonal growth are acquired characters. In *Noetia*, such a mechanism is present in the inturned umbos and opisthogyre condition and in this genus the prosodetic ligament is maintained throughout ontogeny. The prosodetic condition in *Noetiella* and *Noetia* is therefore sympleisomorphic at this taxonomic level. *Noetiella* and *Noetia* may well have a common ancestor but the co-occurrence of *Protonoetia* (ancestral to *Noetia* (MacNeil 1938)) and *Scalenoneotia* in the Middle Eocene indicate that the lineages have been separated from an early stage in the radiation of the Noetiidae.

The earliest noetiids occur in the Cretaceous and those most resembling *Noetiella* are *Breviarca* and *Incanopsis*. In *Breviarca* the ligament is amphidetic and the general form is trapezoidal with slight anterior expansion. *Incanopsis* also possesses an amphidetic ligament but is reduced anteriorly. Intuitively one could argue that *Noetiella* arose from *Breviarca* by the single event of the appearance of the prosodetic ligament. However also in the Cretaceous in the genus *Linter* which has strongly opisthogyre beaks and a prosodetic ligament set in a resilifer. MacNeil (1937) proposed that *Linter* also arose from *Breviarca*. If this is correct then the prosodetic condition and the resilifer have evolved at least twice

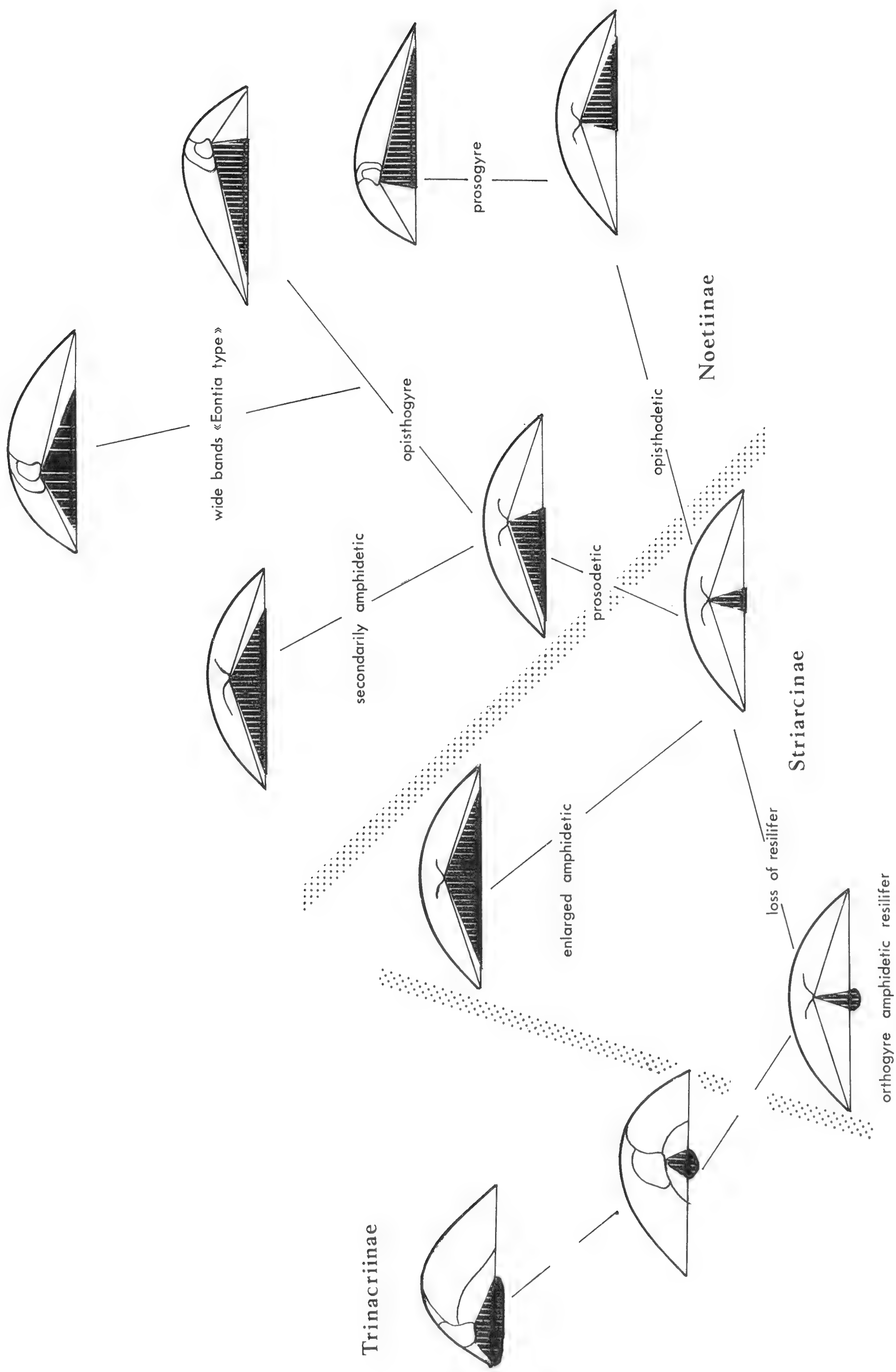


Fig. 13. Evolution of Noetid ligaments — one scheme based on the least number of parallel or repeated events.



during the radiation of the Noetiidae. Both characters appearing independently in *Linter* and the resilifer again in *Arcopsis* and the prosodetic condition again in *Noetiella*. Such repetition is known to have occurred within the Arcacea (Stanley 1972) but this refers specifically to the infaunal-epifaunal oscillations seen in the Parallelodontidae, Grammatodontidae and Arcidae. Within these families the ligament structure varies only in orientation. A resilifer does occur in the Limopsidae (Oliver 1981) and in that family multiple lateral wedges of lamellar ligament can be developed. Thomas (1978) suggested that the noetid ligament can be derived from the limopsid alivincular type and there is a possibility that the earliest noetids possessed a resilifer. If this was the case then there would be less need to invoke repetitive appearance of the resilifer. In Fig. 13 I have illustrated the hypothetical radiation of the noetid ligament starting from an ancestral form with a amphidetic ligament in a resilifer. Such an ancestor may be similar to the Upper Cretaceous genus *Vetoarca* (Stephenson 1947). *Noetiella* therefore can be derived from an amphidetic *Breviarca* type ancestor which itself arose from a *Vetoarca* type ancestor by loss of the resilifer. As indicated in Fig. 13 if this is so then the current subfamily trichotomy is invalid.

#### ACKNOWLEDGEMENTS

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#### LIST OF INSTITUTIONAL ABBREVIATIONS USED IN THE TEXT

BM(NH)	British Museum (Natural History)
MHNP	Museum d'Histoire Naturelle de Paris
ZHMB	Humboldt Museum, Berlin
ZMC	Zoological Museum, Copenhagen
NMW	National Museum of Wales
AMS	Australian Museum, Sydney

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PLATE 24 (opposite)

Fig. 1, 2. *Noetiella congoensis*: periostracum removed (1) L.V., (2) R.V. NMW. Conakry, W. Africa.  $\times 6$ .

Figs. 3, 4. *Noetiella minor*: (3) L.V., (4) R.V. NMW. Basra.  $\times 5$ .

Figs. 5–7. *Noetiella tethyensis*: (5, 6) exterior and interior view of holotype BM(NH) Geol. LL40801,  $\times 4$  (7) exterior view of paratype BM(NH) Geol. LL30083.  $\times 5$ .

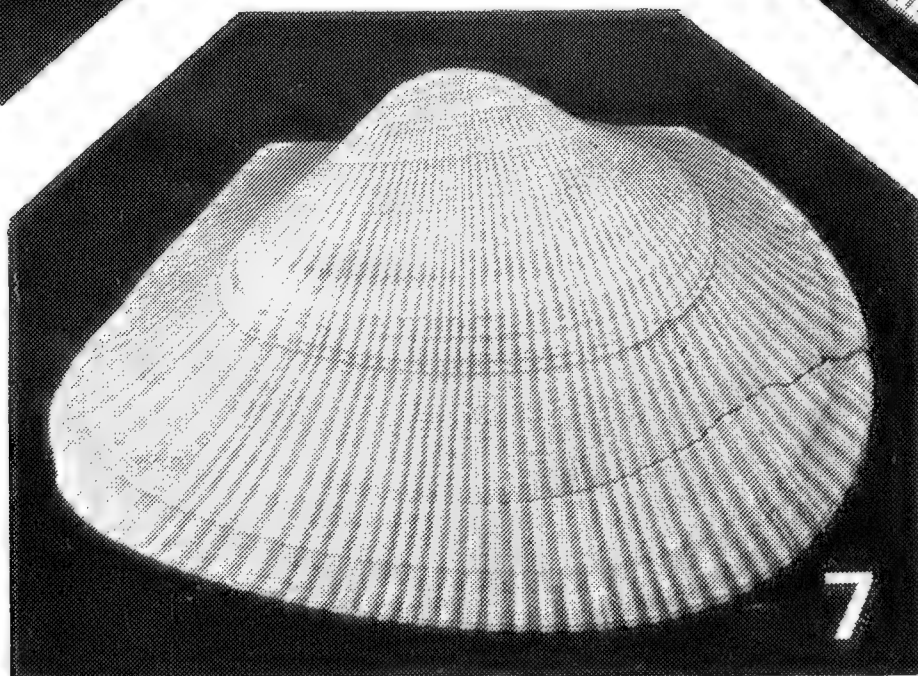
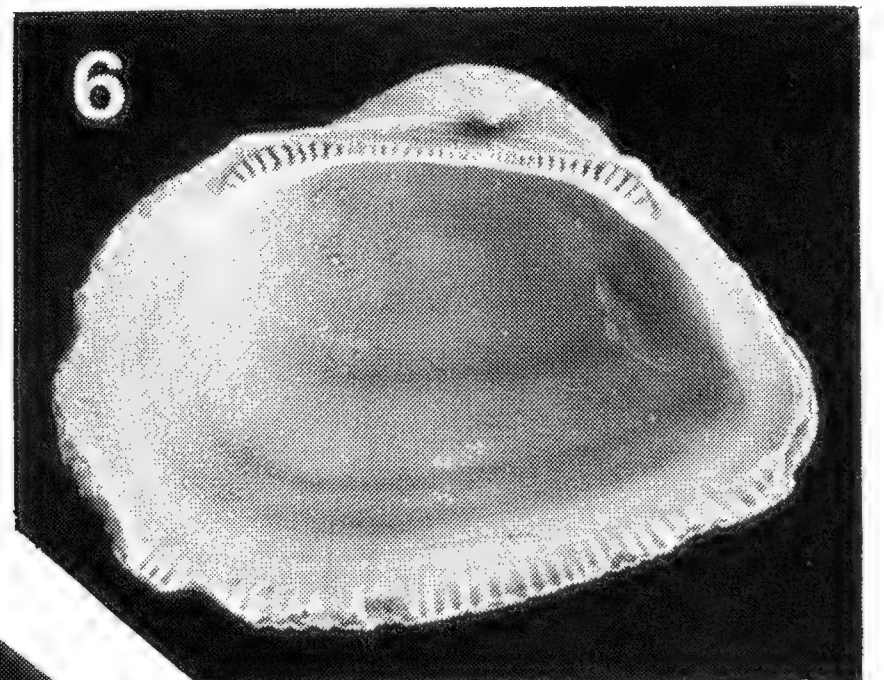
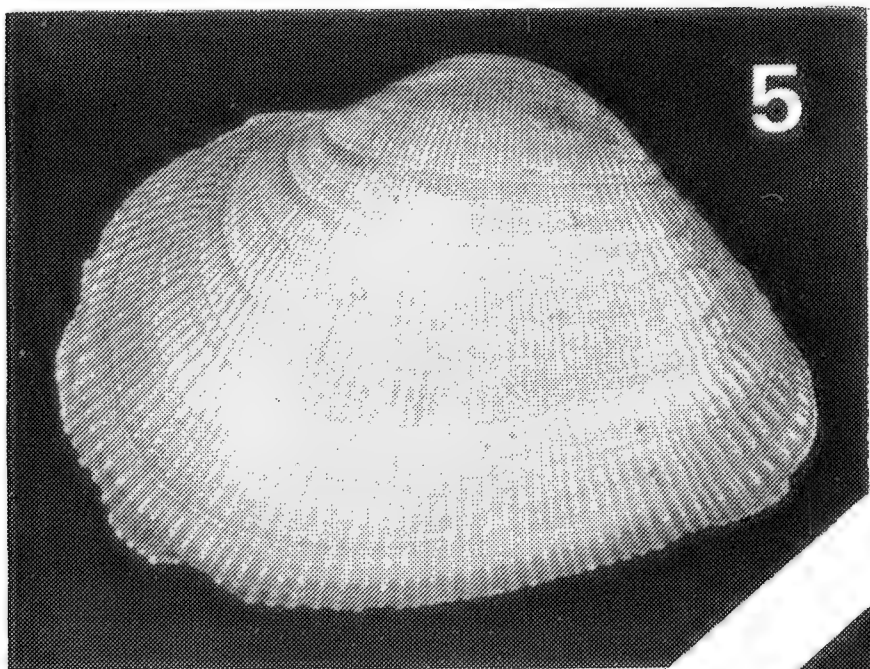
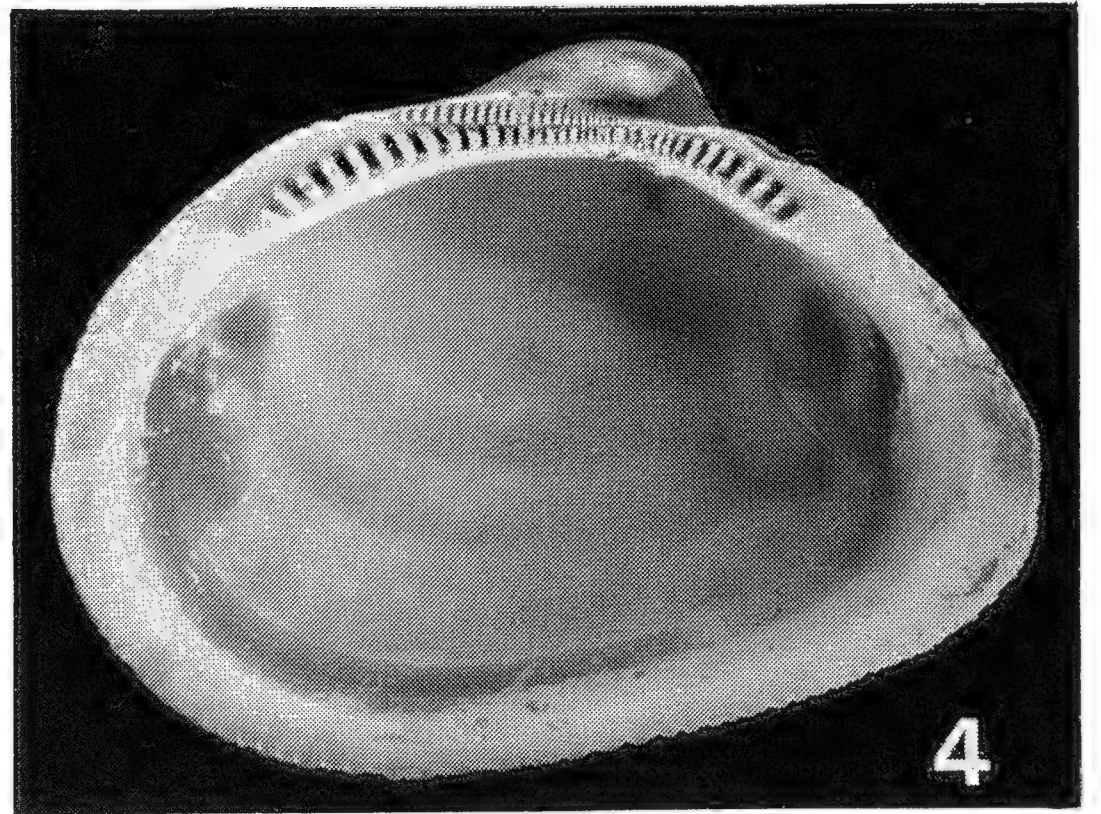
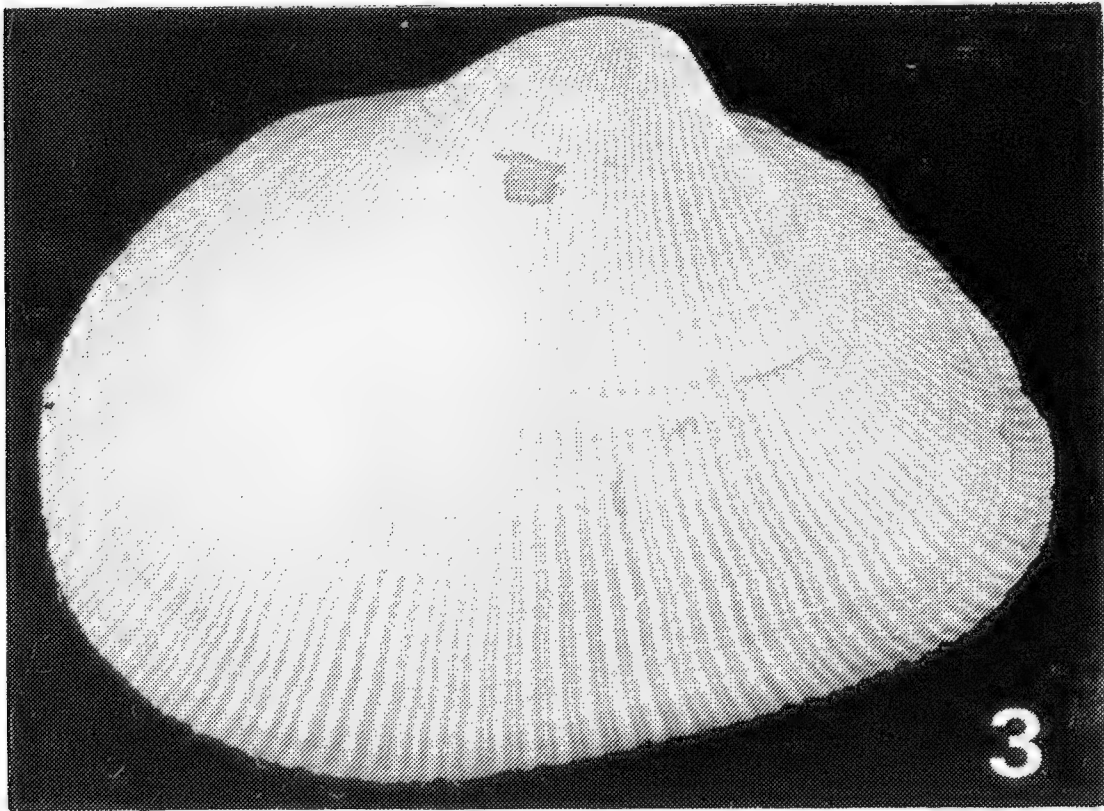
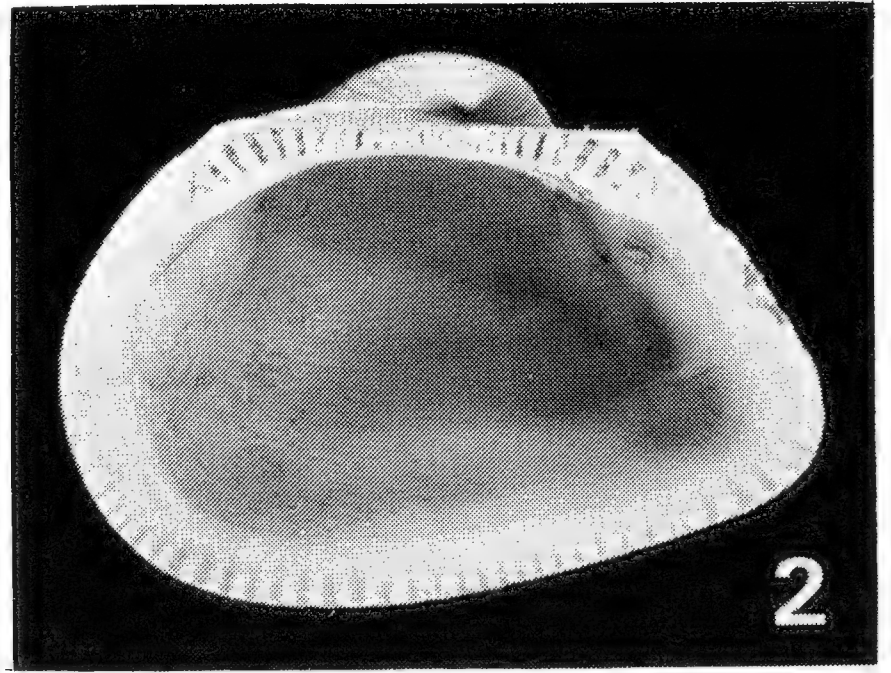
PLATE 25 (overleaf)

Figs. 1–3. *Scalenonoetia africana*: Ameki, Nigeria; (1) L.V., (2) R.V.,  $\times 4$  (3) BM(NH) Geol. L58512.  $\times 5$ .

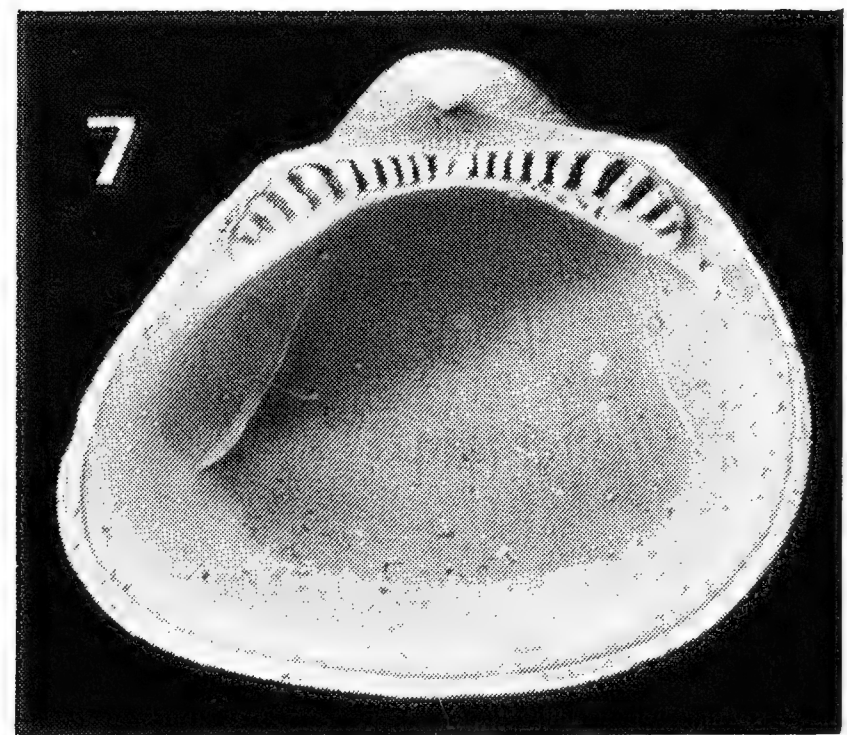
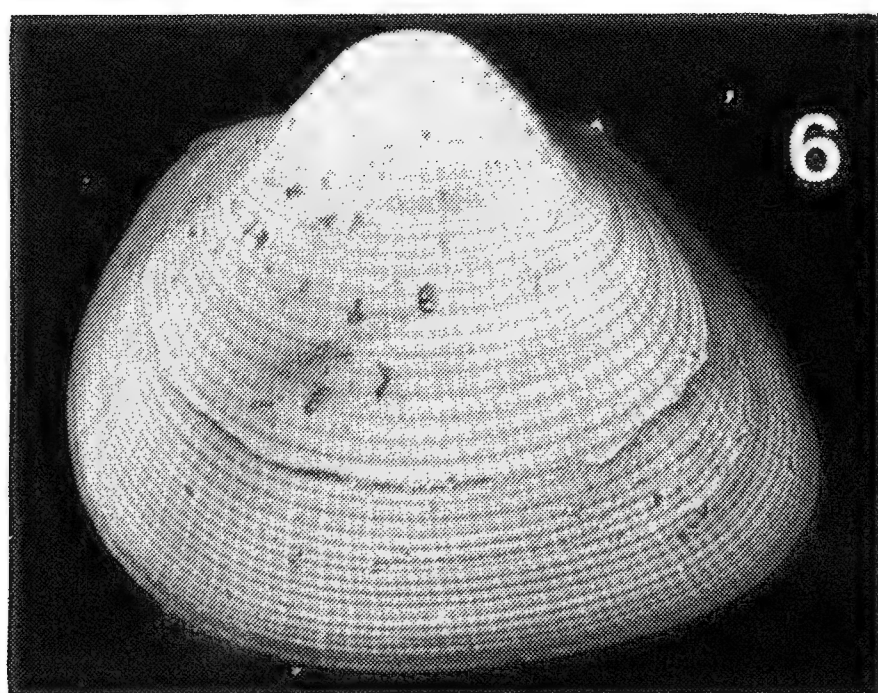
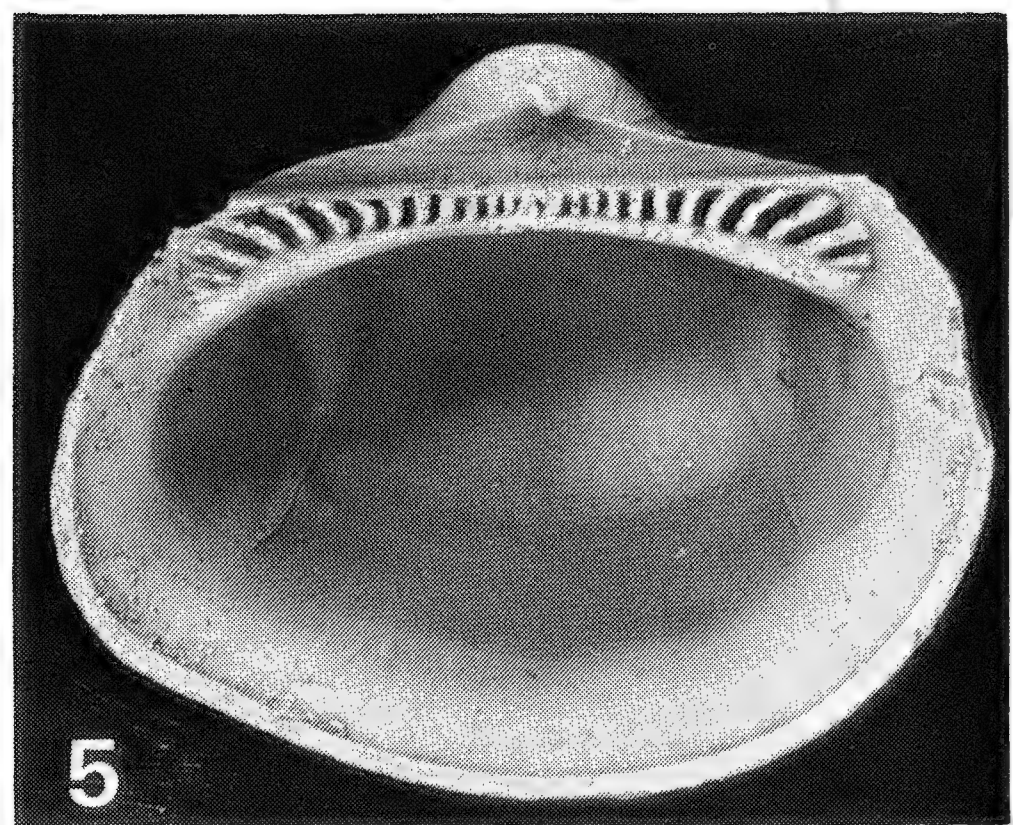
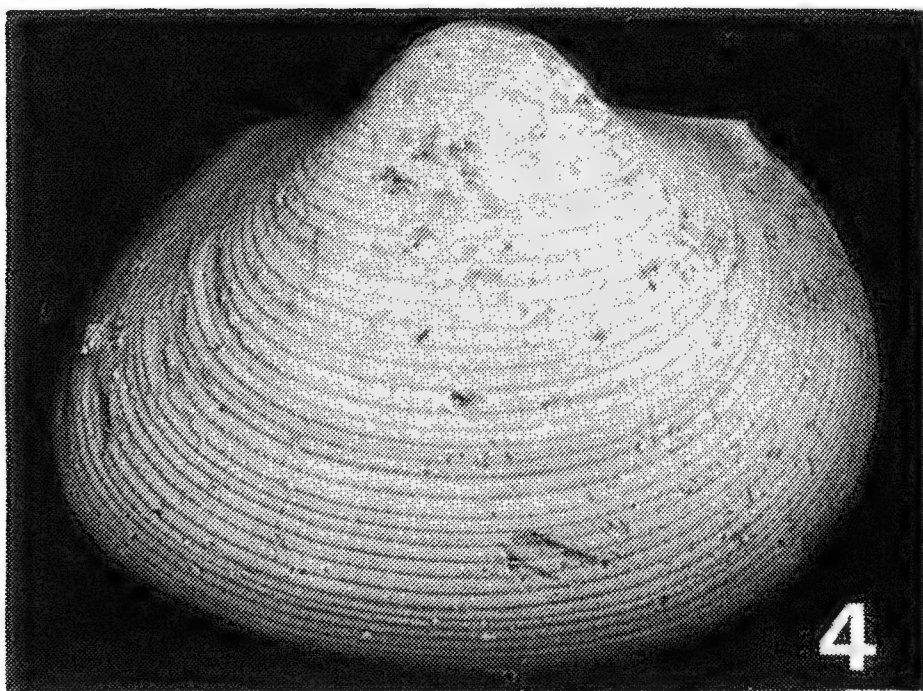
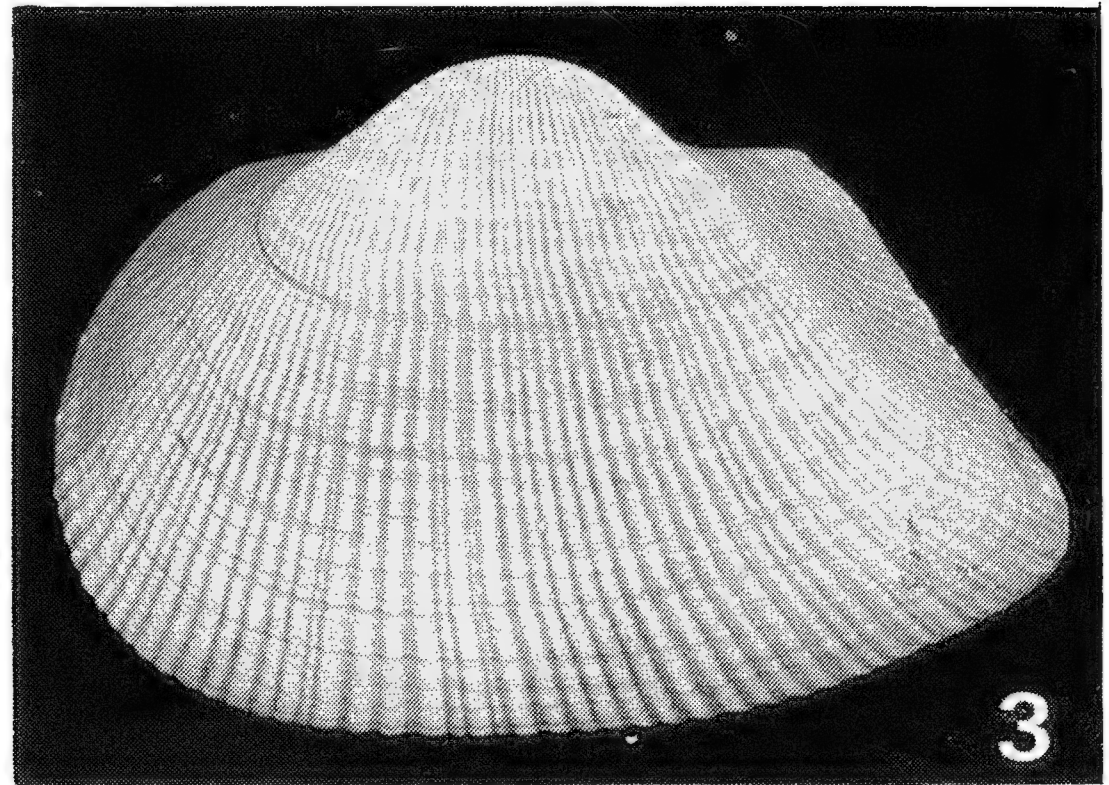
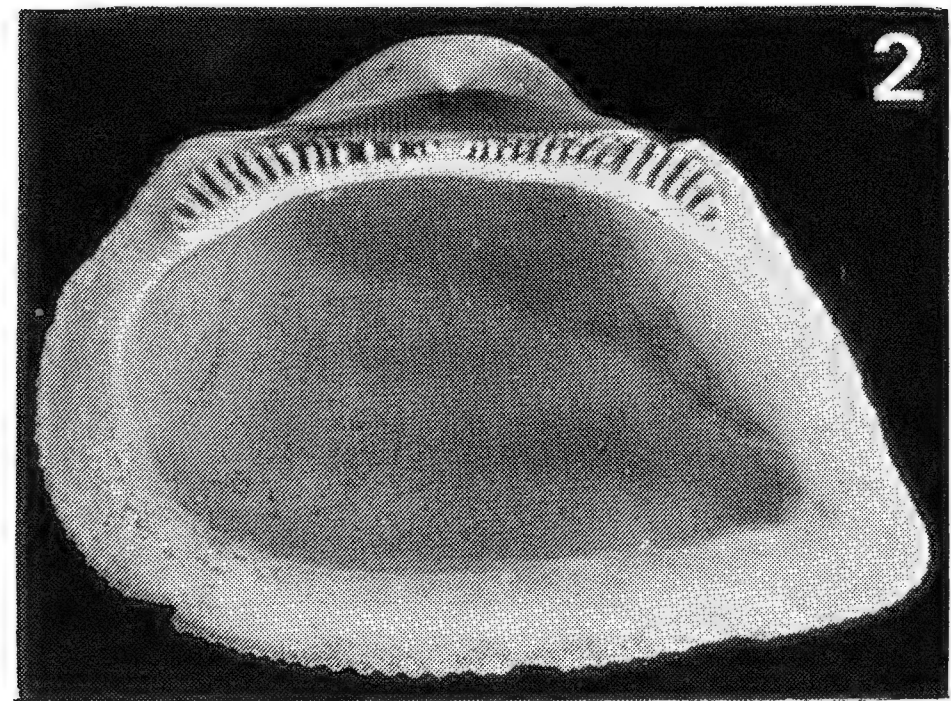
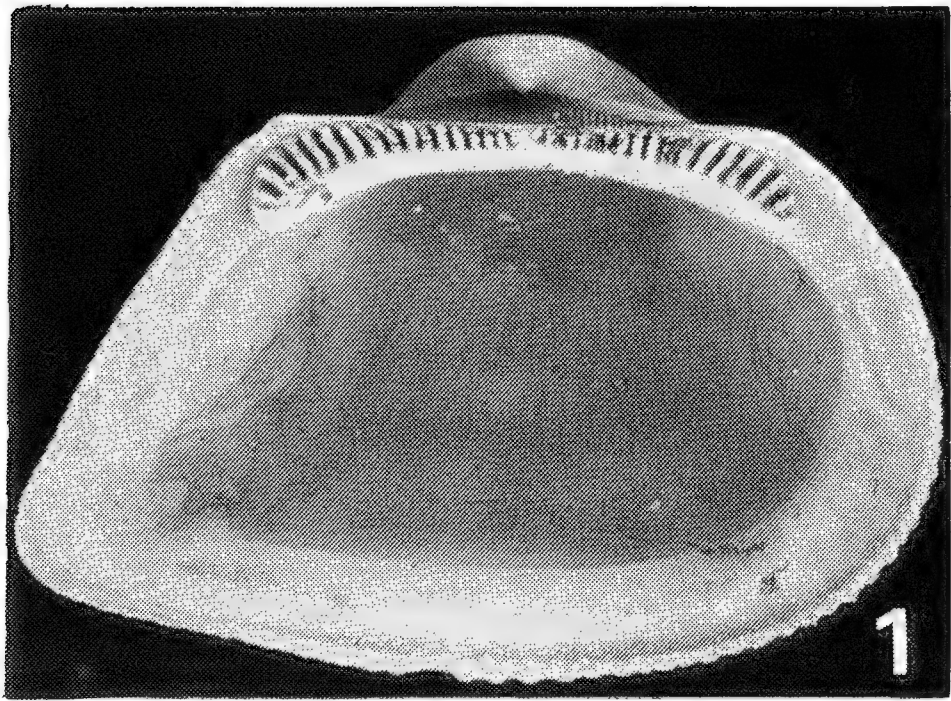
Figs. 4, 5. *Breviarca saffordi*: Coon Creek, Tennessee; (4) interior view of R.V. (5) exterior view of R.V.  $\times 6$ .

Figs. 6, 7. *Breviarca perbrevis*: Coon Creek, Tennessee; (6) exterior view of L.V., (7) interior view of L.V.  $\times 8$ .











# *ESTELLACAR* IREDALE, *RECTANGULARCA* EAMES AND THE SYSTEMATIC POSITION OF *BARBATIA* *PECTUNCULIFORMIS* DUNKER (BIVALVIA, ARCOIDA, NOETIIDAE)

P. GRAHAM OLIVER<sup>1</sup>

(Accepted for publication, 19th April, 1986)

**Abstract:** The functional morphology of the genus *Estellacar* is described and the unusual elliptical form is shown to be an infaunal character. Although the length:height ratio is typical of epibyssate arcoids *Estellacar* displays numerous infaunal traits especially the labial palps which are the largest yet observed in the Arcoida. *Estellacar* is shown to be a valid genus and having close similarities to the Eocene genus *Rectangularca*. The probable phylogeny suggests that any association with *Striarca* or the Striarcinae is artificial. The species are described, and include *E. saga*, *E. olivacea*, *E. galactodes* and *R. africana*. The systematics of '*Barbatia*' *pectunculiformis* (Dunker) are reviewed. Although this species is most like *Estellacar* the differences in shell form are considered to be significant enough to warrant separate generic status, as *Scelidionarca* n. gen.

## INTRODUCTION

An elliptical, non costate shell form is unusual in the Noetiidae but is present in the Recent genus *Estellacar* Iredale (1939) and the Eocene genus *Rectangularca* Eames (1957). Newell (1969) and Habe (1977) regarded *Estellacar* as synonymous with or as a subgenus of *Striarca*. Oliver (1985) expressed doubts about the affinity with *Striarca* but had insufficient data to confirm them. Preserved specimens of *Estellacar* were located in the collections of the British Museum (Natural History) and these have been used to examine the functional morphology and systematic status of the genus. In view of the similarity in form of *Rectangularca* this genus is reviewed in light of the findings on *Estellacar*. *Rectangularca* was not mentioned by Newell (1969). Lynge (1909) suggested that '*Barbatia*' (as *Fossularca*) *pectunculiformis* Dunker (1866) was allied to *Estellacar* (as *Arca*) *olivacea*. However this species has been associated with four other genera and consequently requires revision, before its association with *Estellacar* can be confirmed.

## ANATOMY OF *ESTELLACAR*

From dissection of specimens of *Estellacar galactodes* (Benson) from Foochow, China; British Museum (Natural History).

**Mantle:** The mantle is opaque but rather thin. The mantle edge (Fig. 1) is simple medially and posteriorly but bears small folds anteriorly and well developed folds at the posterior-ventral junction. The posterior folds indicate discreet inhalent and exhalent apertures.

**Ctenidia and labial palps** (Fig. 1): The ctenidia although contorted were like those of other arcoids being homorhabdic, nonplicate and filibranch. The inner demibranch is the slightly larger of the two.

<sup>1</sup> Sub-department of Invertebrate Zoology, National Museum of Wales, Cathays Park, Cardiff CF1 3NP

The labial palps are very large for an arcoid and possess approximately 80–90 fine ridges. There is a narrow oral fold.

*Abdominal region* (Fig. 2): The abdominal organs are small, ovoid structures. The glandular pads overlying the visceral ganglion are well developed and shown some differentiation in structure.

*Foot and musculature* (Fig. 1): The foot is very large with a large toe and small heel. The toe is deep and compressed. A ventral groove is present but no byssus has been observed. The pedal retractors are small as are the pedal protractors.

*Alimentary canal* (Figs. 3, 4): The oesophagus is dorsoventrally flattened, rather short and enters the stomach high on the anterior face. The combined style sac and mid gut leaves the stomach ventrally and passes deep in the foot before forming a short anterior loop, it then curves dorsally in small convolutions but scarcely reaches the right of the stomach before bending back upon itself and passing posteriorly as the hind gut.

The stomach structure is similar to that of other noetids. The food sorting caecum is well developed and is deeply separated from the dorsal hood. The right dorsal protrusion is just discernible and the right ventral tract is represented by a small pouch and a single undeveloped ridge. The style sac is poorly ridged.

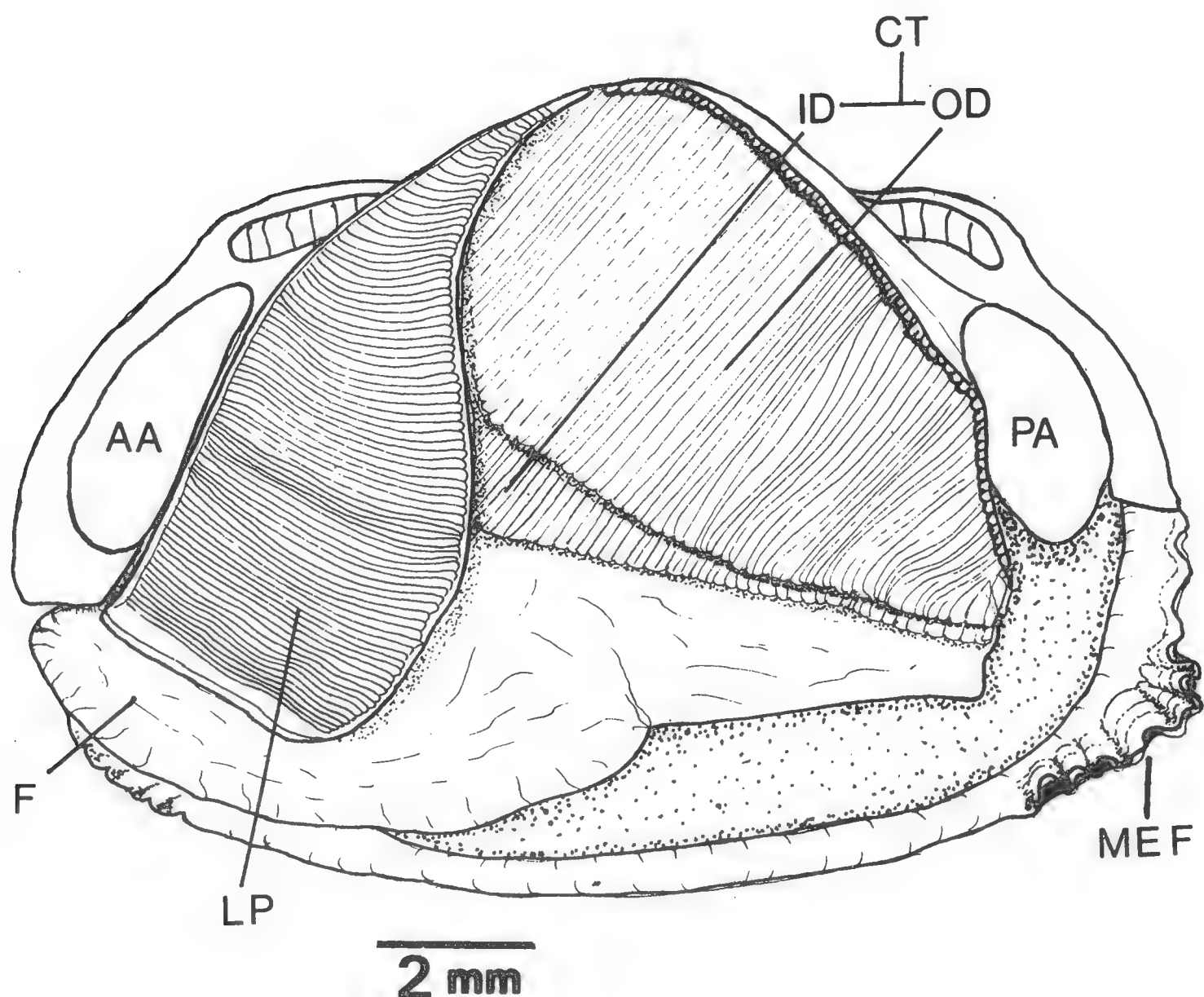


Fig. 1. *Estellacar galactodes* from Foochow, China; Gross anatomy viewed from left side after removal of the mantle.

#### ABBREVIATIONS TO FIGURES

A anus, AA anterior adductor muscle, AO abdominal organ, APR anterior pedal retractor muscle, CT ctenidium, DDD ducts to the digestive diverticula, DH dorsal hood, F foot, FSC food sorting caecum, GA gill axis, GT glandular tissues, H heart, HG hind gut, ID inner demibranch, LP labial palps, MEF mantle edge folds, MG mid gut, OD outer demibranch, OE oesophagus, PA posterior adductor muscle, PPR posterior pedal retractor muscle, RDT right dorsal tract, RVT right ventral tract, SS style sac, VG visceral ganglion.

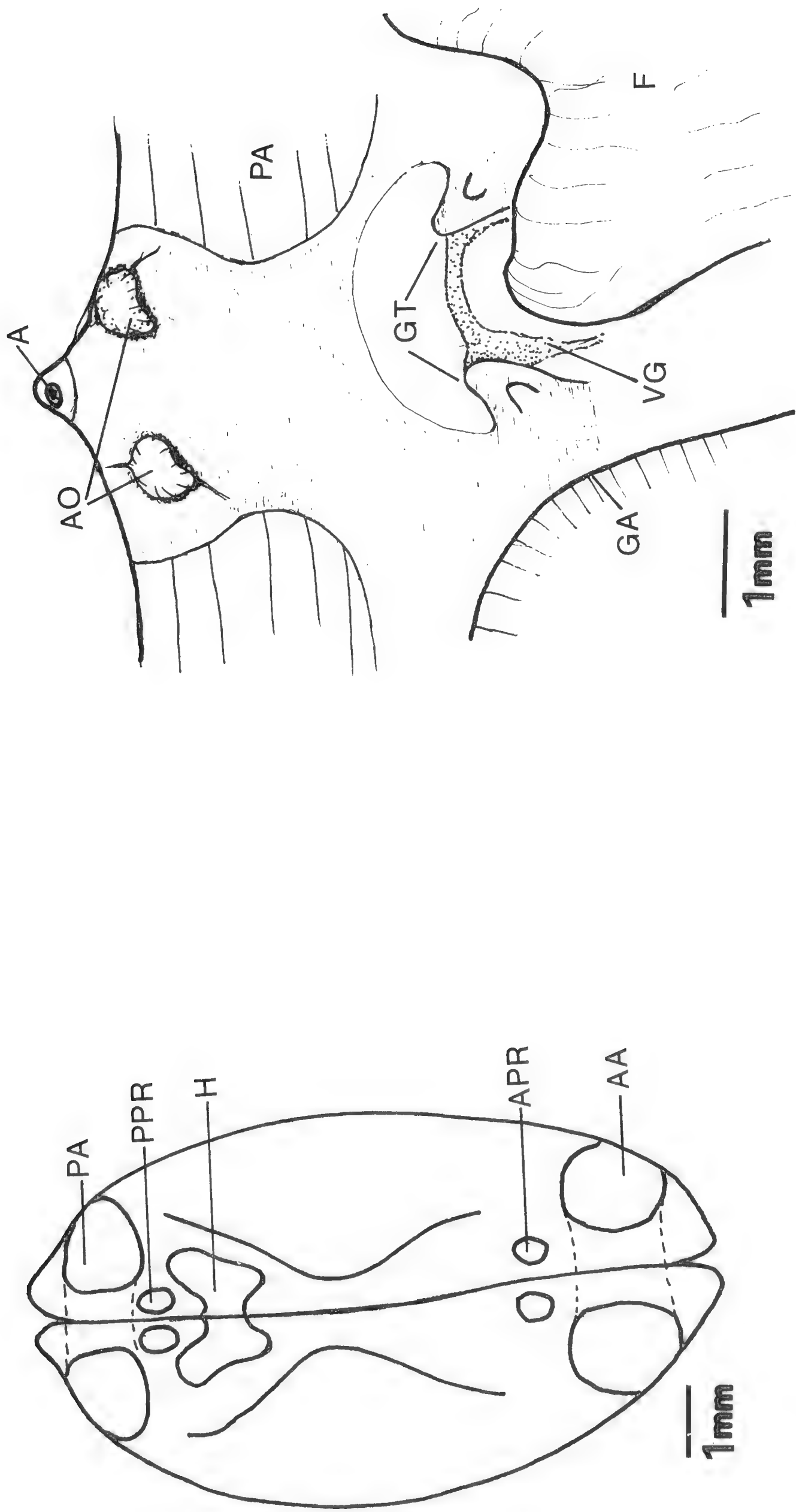


Fig. 2. *Estellacar galactodes* from Foochow, China; Dorsal diagrammatic view to show relative size of adductor and pedal muscles.

Fig. 3. *Estellacar galactodes* from Foochow China; View of the abdominal region.



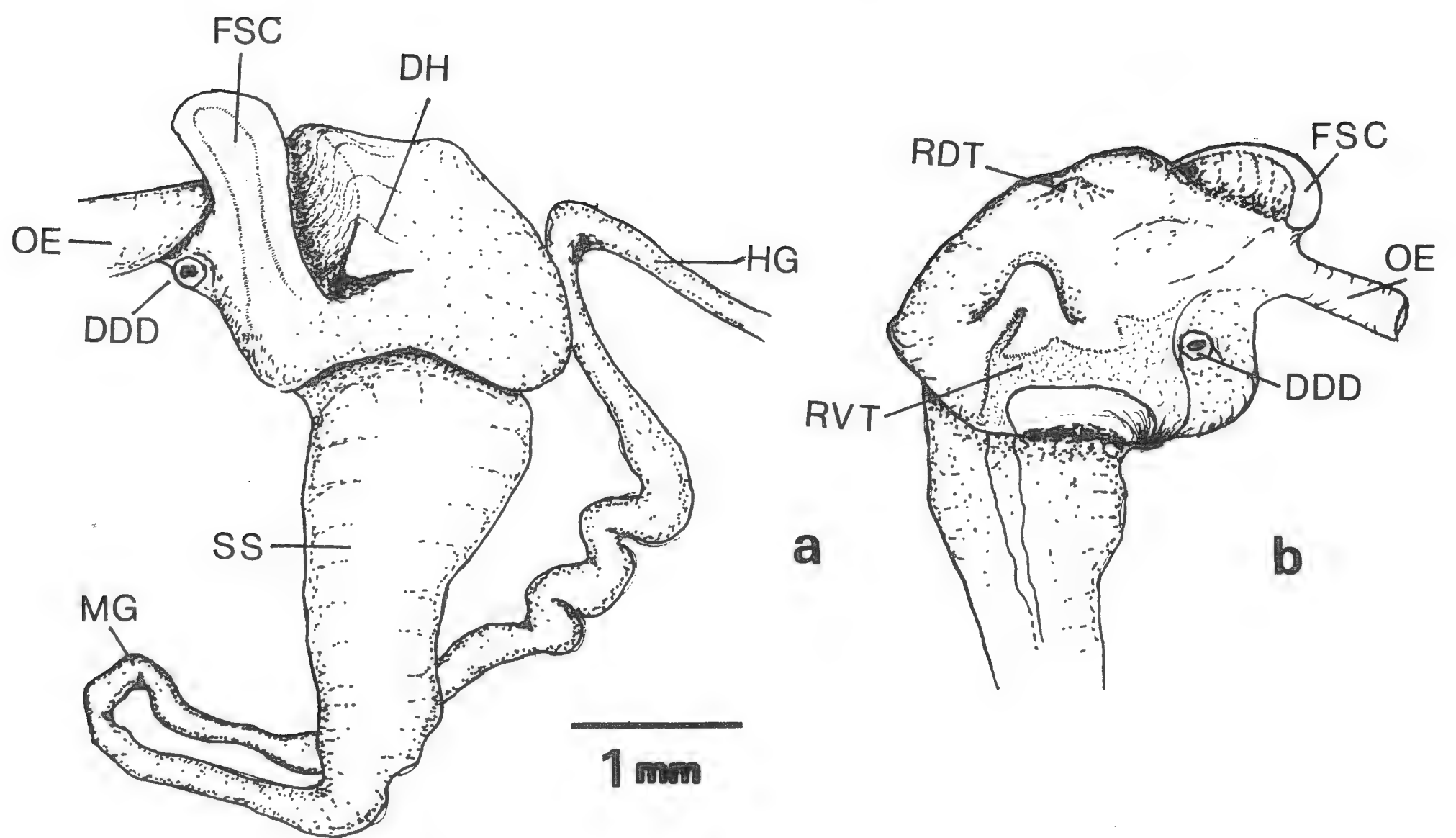


Fig. 4. *Estellacar galactodes* from Foochow China; Stomach (a) from the left side (b) from the right side.

*Remarks:* There are a number of anatomical features which suggest that *Estellacar* is an infaunal genus. The pedal retractors are small and of roughly equal size; in epifaunal arcoids the posterior pedal retractors are usually much larger than the anterior pair and reflect their function as byssus retractor muscles. The foot is compressed and the toe is large reflecting the burrowing function. In epifaunal genera such as *Striarca* or *Arcopsis* the toe and heel are elongate giving the foot a long sole on which the animal can crawl. The lack of byssus is of course indicative of an infaunal existence, but in preserved specimens it cannot be relied upon to have been retained. The mantle edge folds are weak except at the post-ventral junction where they act to form inhalent and exhalent apertures. In epifaunal species the mantle edge is folded along a greater length (see *Striarca* vs *Verilarca* in Oliver 1985). Heath (1941) Lim (1966) and Oliver (1985) illustrated that infaunal species tend to have larger labial palps than epifaunal species. The labial palps of *Estellacar* are proportionately the largest yet recorded in the Arcacea and is further evidence of the infaunal habit.

The shell also reflects some infaunal features, notably the periostracum which consists of short erect hairs. Epifaunal genera such as *Striarca* or *Barbatia* have flat linear bristles which protect the gaping edges of the valves. There is also the lack of any byssal notch or median sinus, if present both would indicate the use of a substantial byssus. The elliptical outline is not indicative of an infaunal existence as most infaunal species are trapezoidal. However *Estellacar* is virtually equilateral which is not the case for epifaunal forms which normally have a reduced anterior area. The weak radial sculpture is unusual for epifaunal and infaunal arcaceans, most being costate. Costate, trapezoidal infaunal species generally inhabit unstable substrates where both characters aid in preventing the animal from being dislodged from the substrate. Some of the records of *Estellacar* suggest that the preferred habitat is tranquil muddy substrates (eg. Ennur Backwater and Canals on Chusan Is.) and if this is generally true then the costae would be redundant. One conflicting observation with the infaunal habit is the height:length ratio which varies from 1.47–1.75 and is greater

than the 1.35 ratio cited by Stanley (1970), Thomas (1978) and Oliver and Allen (1980) as the upper range for infaunal arcoid species. The length:height ratio of *Estellacar* is in the range of that given by Thomas (1978) for *Barbatia*. However barbatiaform arcoids possess all the epibyssate characters cited above as being absent in *Estellacar* and I can only surmise that the 1.35 height:length ratio is applicable only in trapezoidal species. The elliptical form of *Estellacar* is an exception because the adaptive features of the trapezoidal form are redundant in soft very stable substrates.

## SYSTEMATICS

### **Estellacar** Iredale, 1939

Type species *Estellacar saga* Iredale, 1939

Small to moderately sized shells reaching 40 mm in length, equivalve, slightly inequilateral, the anterior area is slightly expanded. Outline elliptical, longer than high, anterior margin rounded, posterior margin rounded or gently curved only slightly truncate in some specimens, ventral margin gently curved with no byssal gape or sinus. Moderately inflated. Umbos low, orthogyre – very slightly opisthogyre, dorsal area long, narrow and cleft. Ligament amphidetic with narrow vertical fibrous and lamellar strips. Sculpture of concentric lines crossed by numerous fine radial costellae which may become obsolete except at the margins. Periostracum thick, dark brown, developed into short, fine erect spines at the intersection of the sculptural elements. Hinge weak, teeth small, almost vertical, in two poorly defined series. Adductor scars subequal, the anterior slightly longer, both with very weak myophoric ridges. Pedal retractor scars of equal size. Inner margins smooth.

*Distribution:* Recent, Indo-Pacific.

*Remarks:* The functional morphology of *Estellacar* shows that this genus is infaunal and therefore quite unlike *Striarca*. Oliver (1985) also redescribed the infaunal genus *Verilarca* but that genus is trapezoidal and costate again quite unlike *Estellacar*. An association with *Striarca* or *Verilarca* may be valid if there was any evidence that *Estellacar* had evolved from that stock in the Neogene. However the most similar taxon is found in the Middle Eocene suggesting that the *Estellacar* and *Striarca* lineages diverged early in the radiation of the Noetiidae. This Eocene taxon is *Rectangularca africana* (Newton 1922). Eames (1957) erected *Rectangularca* distinguishing it from *Striarca* and *Breviarca* but in view of its similarity with *Estellacar* this paper presents the following differential diagnoses.

### **Rectangularca** Eames, 1957

Type species: *Striarca africana* Newton, 1922

Small shells, reaching 20 mm in length, left valve with a weak submarginal groove suggestive of an inequivalve condition. Equilateral. Outline elliptical, much longer than high, anterior margin curved, posterior margin almost straight, ventral margin gently curved with no byssal gape or median sinus. Moderately inflated. Umbos, low orthogyre – very slightly opisthogyre, dorsal area, long narrow, and slightly angled to form a central ridge. Ligament amphidetic with narrow fibrous and lamellar strips. Sculpture of concentric lines crossed by numerous costellae. Hinge weak, teeth small, almost vertical in two poorly defined series. Adductor scars subequal, the posterior with a very weak myophoric ridge. Pedal retractor scars of equal size. Inner margins smooth.

*Distribution:* Middle Eocene, Nigeria.

*Remarks:* Although obviously similar to *Estellacar* I would retain the generic status because of the inequivalve and angled dorsal area characters. Functionally *Rectangularca* was probably infaunal as there are no characters either of the muscle scars or outline which

would suggest an epibyssate habit. Of functional interest is the angled dorsal area as this arrangement is opposite to the cleft dorsal area in *Estellacar*. Thomas (1978) in referring to the weak arcoid ligament noted adaptations which reduce dorsal splitting of the ligament. One of these is the cleft dorsal area which effectively reduces the amount of umbonal separation. The opposite arrangement in *Rectangularca* would seem to increase umbonal separation and enhance dorsal splitting which would result in a very weak ligament. Weak ligaments in the Arcoida are the cause of the limited radiation into the infaunal habitat (Thomas 1978) and therefore suggest that *Rectangularca* must have lived in very tranquil soft muds where ligament strength for burrowing would be least required.

Eames (1957) cited only the ventral curvature as the separating character from *Breviarca*, the shared inequivalve condition may suggest some closer link. The inequivalve condition is not found in Recent or Neogene noetids but is found in some Eocene species and many Upper Cretaceous species assigned to genus *Breviarca*. Although species of *Breviarca* are not elliptical some do possess weak radial sculpture, and weak myophoric ridges eg. subgenus *Sanoarca* (Stephenson 1953) (Pl. 26, fig. 8). Elongation of the *Sanoarca* form would lead directly to *Rectangularca*. This link to the Upper Cretaceous is a further indication that the *Estellacar/Rectangularca* lineage is totally separate from that of *Striarca* and that any affinity even at the subfamily level is unwarranted. As with *Noetiella* (Oliver 1987) the traditional subfamily divisions are unable to reflect the radiations observed.

#### SPECIFIC SYSTEMATICS

Specimens of *Estellacar* are not common in museum collections and as a consequence variation is difficult to assess. Variation is found in the shell thickness, tumidity and expression of the radial sculpture. This could be due to ecophenotypic variation or geographic variation. Without large series from a wide variety of localities it is not possible to be definitive and consequently the three previously described species are retained. Should this variation be ecophenotypic then there would be but a single species which would take the name of *Estellacar galactodes* (Benson 1842).

**Estellacar saga** Iredale, 1939 (Pl. 26, fig. 2)

*Material Examined*: 1 valve, Seaforth, Mackay, N. Queensland AMS.C94321; 6 valves, Gladstone Harbour, Queensland, AMS.C140418.

SPECIMEN	LENGTH	HEIGHT	L:H	TUMIDITY— SINGLE VALVE	L:T (AS 2 VALVES)
AMS C94321	39.40	24.00	1.64	9.20	2.14
AMS C140418	22.60	14.35	1.57	5.95	1.90
	20.60	12.80	1.61	4.90	2.10
	19.50	12.10	1.61	4.80	2.03
	18.15	11.60	1.56	4.20	2.16
	17.40	10.70	1.63	4.35	2.00
	15.60	9.80	1.59	3.60	2.17
			x=1.60		x=2.07

*Description*: As for the genus but reaches the largest size, has greater anterior expansion and more truncated posterior. The radial sculpture is expressed as costellae and these are spaced at 3–4 per millimetre length.

**Estellacar galactodes** (Benson, 1842)

(Pl. 26, figs. 1, 3: Pl. 27, fig. 1)

*Material examined:* 3 specimens, Foochow, China coll. Cheng BM(NH): 3 specimens, Sandwich Islands (Hawaii) coll. Cuming BM(NH) Acc. no. 1829.

1 specimen, Chusan Island, China. coll. Benson UCZM – Macandrew.

SPECIMEN	LENGTH	HEIGHT	L:H	TUMIDITY	L:T (AS 2 VALVES)
coll. Cheng	17.30	11.80	1.47	10.00	1.73
	17.10	11.10	1.54	9.60	1.78
coll. Cuming	20.55	14.45	1.42	11.90	1.73
	19.90	13.35	1.49	12.50	1.59
	16.55	10.60	1.56	8.70	1.89
			x=1.50	x=1.74	

*Description:* These specimens are similar in outline to *E. saga* but are less elongate, L:H (x=1.50) as opposed to L:H of 1.60, and more tumid L:T (x=1.74) as opposed to an L:T of 2.07. The radial sculpture is similarly spaced at 3–4 costellae per millimeter length but is more strongly expressed over the whole shell. The periostracum is very thick and the bristles are well developed.

*Remarks:* For a more detailed description of the types see Benson (1855). The specimens from China were collected from estuarine or brackish water habitats. Cantor (1842) suggested that his specimens were taken from canals which connected to the sea. This leads me to suspect that the locality “Sandwich Island” appended to the Cuming material is erroneous.

**Estellacar olivacea** (Reeve, 1844)

(Pl. 26, figs. 5,7: Pl. 27, fig. 2)

*Material examined:* 3 specimens (SYNTYPES), Cebu, Philippines, BM(NH) 1969245.

3 specimens, Cebu, Philippines, NMW:1955.158

1 specimen, Ennur Backwater, India, BM (NH) 1953.1.23.474.

SPECIMEN	LENGTH	HEIGHT	L:H	TUMIDITY	L:T
BM(NH) 1969245	16.05	10.40	1.54	9.55	1.68
	21.40	13.40	1.59	10.50	2.03
	16.70	10.80	1.55	10.00	1.67
NMW:1955.158	17.40	11.40	1.53	8.40	2.07
	19.50	12.60	1.55	9.20	2.12
	19.20	12.20	1.57	9.50	2.02
BM(NH) 1953.1.23.474	9.50	5.85	1.62	4.80	1.98
			x=1.56	x=1.94	

*Description:* *E. olivacea* is the most elliptical in form with little difference in curvature of the posterior and anterior margins. It is relatively thin shelled, and with a weaker hinge. The radial sculpture is poorly expressed and takes the form of fine raised lirae which are spaced at 8–9 per millimetre length. The periostracum is thin and the bristles are minute.

**Rectangularca africana** (Newton, 1922)

(Pl. 26, figs. 4, 6)

*Material examined:* Lectotype Cutting 6, Ameki, E. Nigeria BM(NH) Paleontology L.48172; Paralectotypes all from same site: Cutting 5, L48169; Cutting 6, L48173, L48174–8; Cutting 10, L48164–8; Cutting 12, L48170; Cutting 14, L48171.



SPECIMEN	LENGTH	HEIGHT	L:H	TUMIDITY- (SINGLE VALVE)	L:T
L48171	19.15	10.20	1.88	4.75	2.02
L48164	17.35	8.40	2.06	3.85	2.25
L48165	10.25	5.80	1.77	2.40	2.14
L48166	7.10	4.10	1.73	1.50	2.36
L48167	7.60	4.30	1.77	1.80	2.11
L48168	7.90	4.60	1.65	1.80	2.19
			x=1.81		x=2.18

Description as for the genus, the radial sculpture consists of costellae and lirae spaced at 4–6 per millimetre length, medially the costellae are interspaced with 2 lirae but laterally only costellae are present.

### ***Barbatia pectunculiformis* Dunker, 1866**

This paper now turns to the problematic species '*Barbatia* *pectunculiformis* Dunker. Although associated with *Estellacar olivacea* by Lynge (1909) this was questioned by Lamy (in Pallary 1939). Specimens are very scarce and I have been able to examine only the holotype and one other valve. Despite this I have concluded that *Barbatia pectunculiformis* is most similar to *Estellacar* and present it in this paper. For reasons that will be explained this species is given separate generic status.

### ***Scelidionarca* gen. nov.**

Type species: Monotypic *Barbatia pectunculiformis* Dunker, 1866

*Generic Diagnosis:* Shell small to 27 mm in length, equivalve, inequilateral being expanded anteriorly and somewhat truncate posteriorly, length only slightly greater than height, anterior margin broadly curved, ventral margin curved but almost straight, posterior margin straight. Umbos low very slightly opisthogyre. Dorsal area short and cleft, narrow. Ligament amphidetic. Sculpture of concentric lines crossed by numerous radial raised lirae spaced at 6–7 per millimetre length. Periostracum dark brown, persistent, thickened at the intersections of the sculptural elements. Hinge plate short, gently curved, teeth becoming chevron shaped laterally. Adductor scars subequal, the anterior being slightly larger. Inner margins smooth.

*Distribution:* Recent, Indo Pacific.

*Etymology:* Skelidion, (Greek) diminutive of rib referring to the weak radial sculpture.

### ***Scelidionarca pectunculiformis* Dunker, 1866**

(Pl. 27, figs. 3, 4)

*Barbatia pectunculiformis* Dunker, 1866; p. 88–89, pl. 28, figs. 4–6.

*Barbatia pectunculiformis* Kobelt, 1891; p. 125–126, pl. 32, figs. 5–6.

*Noetia pectunculiformis* Lamy, 1907; p. 300–301.

Not *Fossularca pectunculiformis* Lynge, 1909; p. 115.

Not *Noetia pectunculiformis* var *minor* Pallary, 1939; p. 125–126.

SPECIMEN	LENGTH	HEIGHT	L:H	TUMIDITY (SINGLE VALVE)	L:T
BM(NH) 1969257 (Holotype)	27.15	21.15	1.28	7.30	1.86
NMW 1955.158	18.85	15.00	1.26	4.75	1.98

*Remarks:* The shell of *Scelidionarca* is a more typical trapezoidal form, the broad anterior, lack of byssal sinus, subequal retractors are all indicative of an infaunal habit. The length: height ratio agrees with those for other trapezoidal forms in being less than 1.35.

Stevenson (1972) synonymised *S. pectunculiformis* with *Striaca afra*. Oliver (1985) showed that this latter species is referable to *Arcopsis* and as such can in no way be likened to *Scelidionarca*. Lynge (1909) cited *S. pectunculiformis* but Oliver (1985) showed these specimens were referable to *Verilarca* and *Spinearca*. Other infaunal genera which have been associated with *Scelidionarca* are *Noetiella* (Thiele and Jaeckel 1931, Reinhart 1935) and *Halonanus* (Stewart 1930). Both genera are similar in outline but *Noetiella* possesses a costate shell and prosodetic ligament (Oliver 1987).

*Halonanus* (Pl. 27, fig. 5) is similar to *Scelidionarca* but as MacNeil (1938) demonstrated the ligament is both prosodetic and set in a resilifer. *Halonanus* is therefore akin to *Trinacria*. The sculptural pattern of *Scelidionarca* is most like that of *Estellacar* and both genera also share the dark coloured persistent periostracum. The amphidetic ligament set across a cleft dorsal area is another character shared by these genera. *Estellacar* is almost elliptical and not trapezoidal as in *Scelidionarca* although some of the larger specimens of *E. saga* do show some posterior truncation. If one could rely solely on the sculptural and periostracal characters to associate *Scelidionarca* with *Estellacar* then the resolution of the systematic position would be clear. However, the general form of *Estellacar* is represented in the Eocene by *Rectangularca* and there is no indication at that time of the trapezoidal *Scelidionarca*. Furthermore the dark periostracum and fine sculpture is not unique to *Estellacar* and *Scelidionarca* but is also present in the genus *Didimacar* especially *D. nigra* (Lamy). *Didimacar* is anteriorly reduced, has an opisthodetic ligament and is byssate in habit. Of the two species of *Didimacar*, *D. nigra* is modioliform and has a much weaker sculpture than the barbatiaform *D. tenebrica* (Rve). The weak radial sculpture may therefore be related to the infaunal habit and have little phyletic significance. In conclusion I have simply associated *Scelidionarca* with *Estellacar* because both are infaunal, both share sculptural, ligament and periostracal characters. The general form of *Scelidionarca* is however quite different from *Estellacar* and without phyletic information to associate them closer I feel that *Scelidionarca* should be recognised at the generic level.

#### INSTITUTIONAL ABBREVIATIONS USED IN THE TEXT

BM(NH)	British Museum (Natural History)
NMW	National Museum of Wales
AMS	Australian Museum, Sydney
UCZM	University of Cambridge, Zoological Museum

#### ACKNOWLEDGEMENTS

I would like to thank Noel and Solene Morris for their helpful discussions and for the loan of material from the BM(NH). Also thanks to Dr. Winston Ponder for the loan of material from the Australian Museum. Thanks also to Carol Davies for patiently constructing the typescript and to Mr E. Broadbent for photographs 1–3 on Pl. 27.

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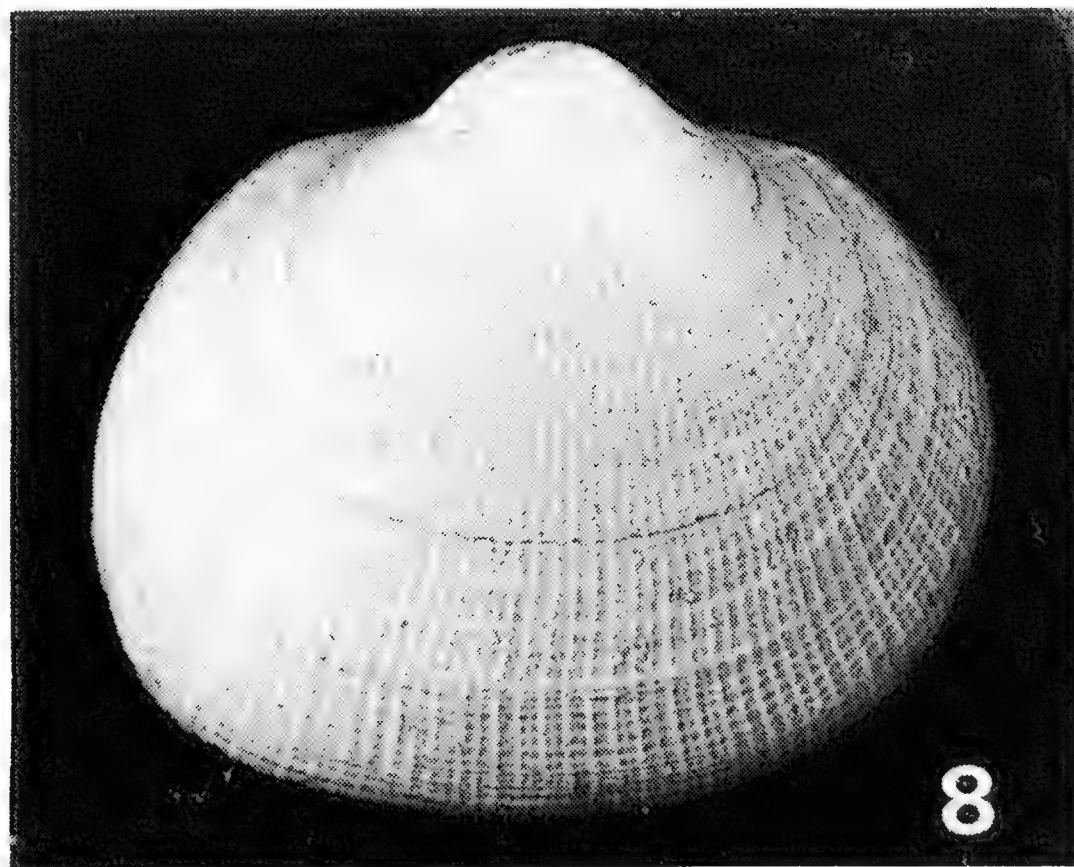
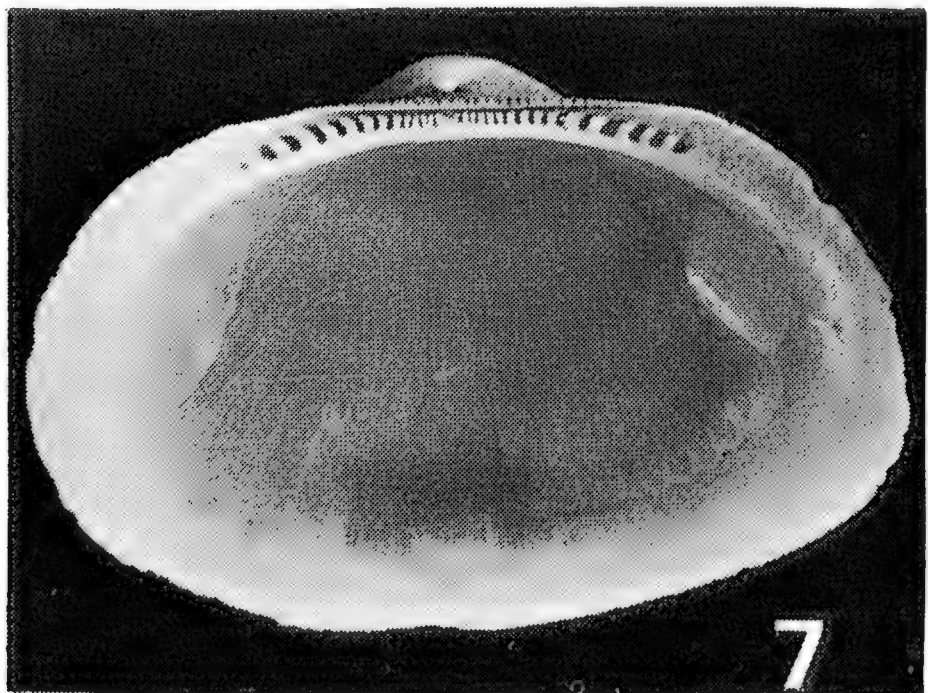
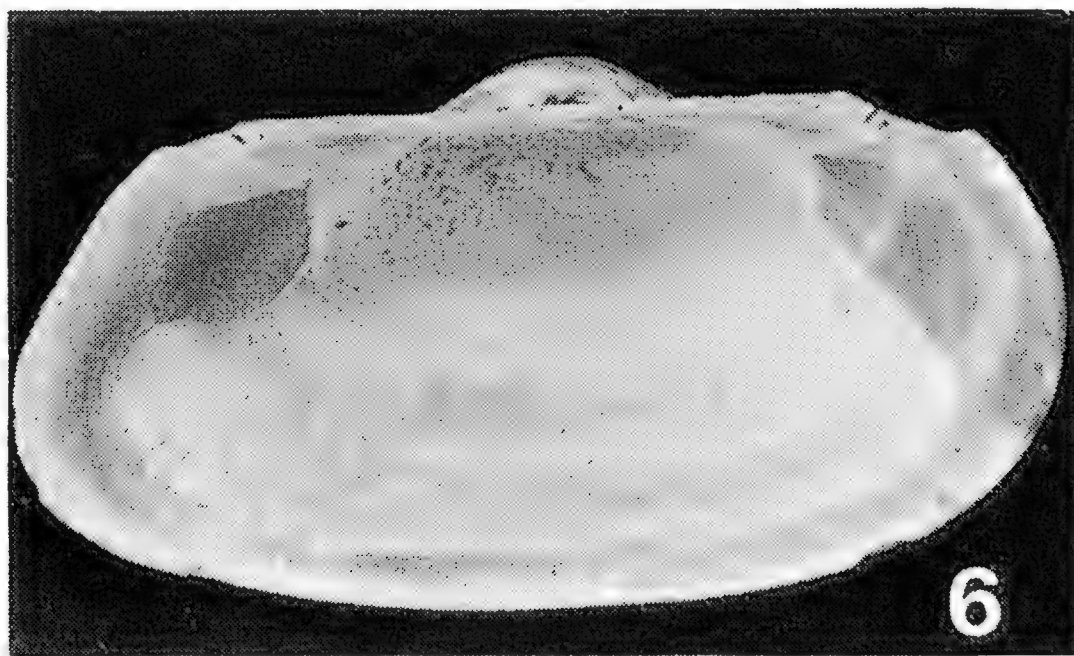
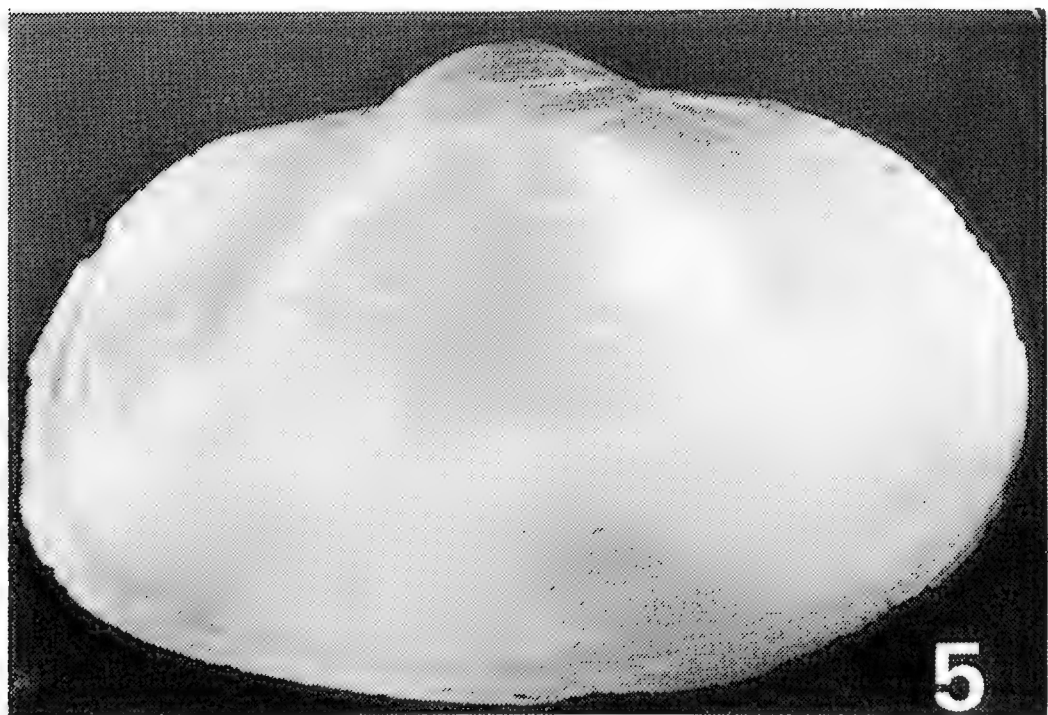
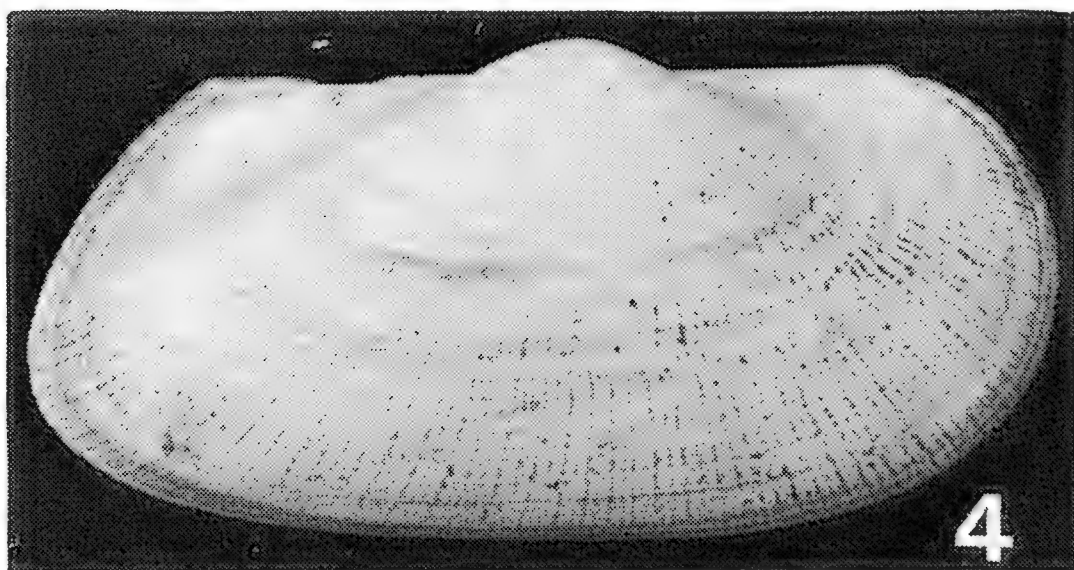
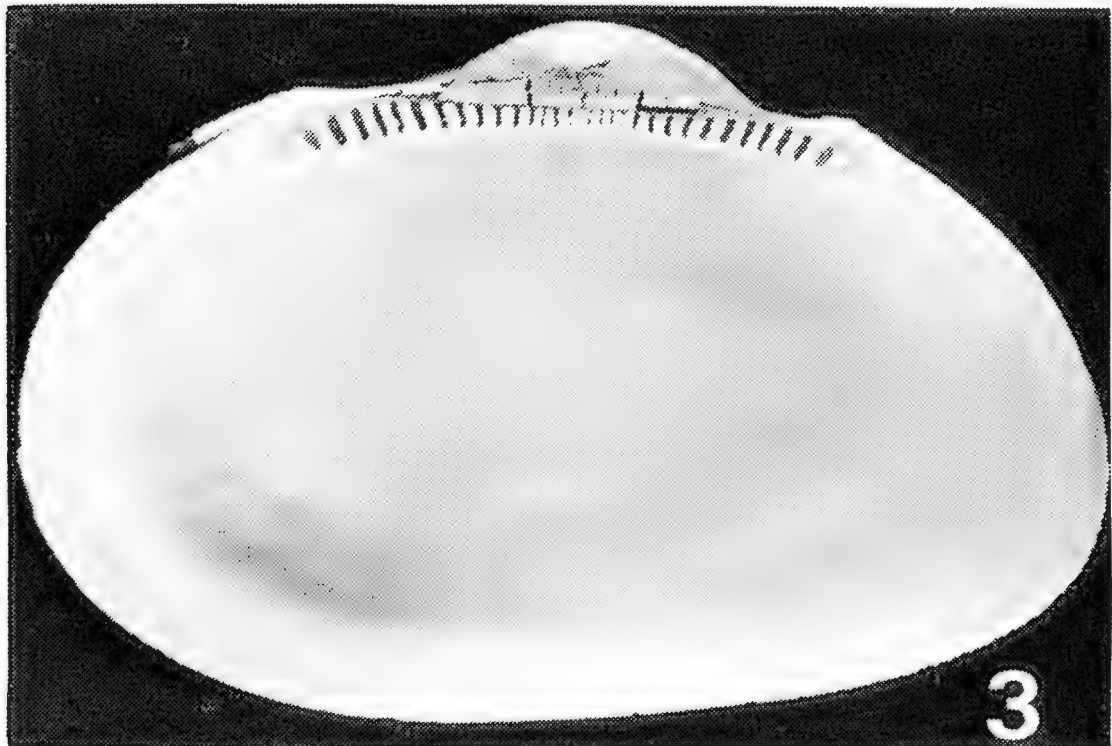
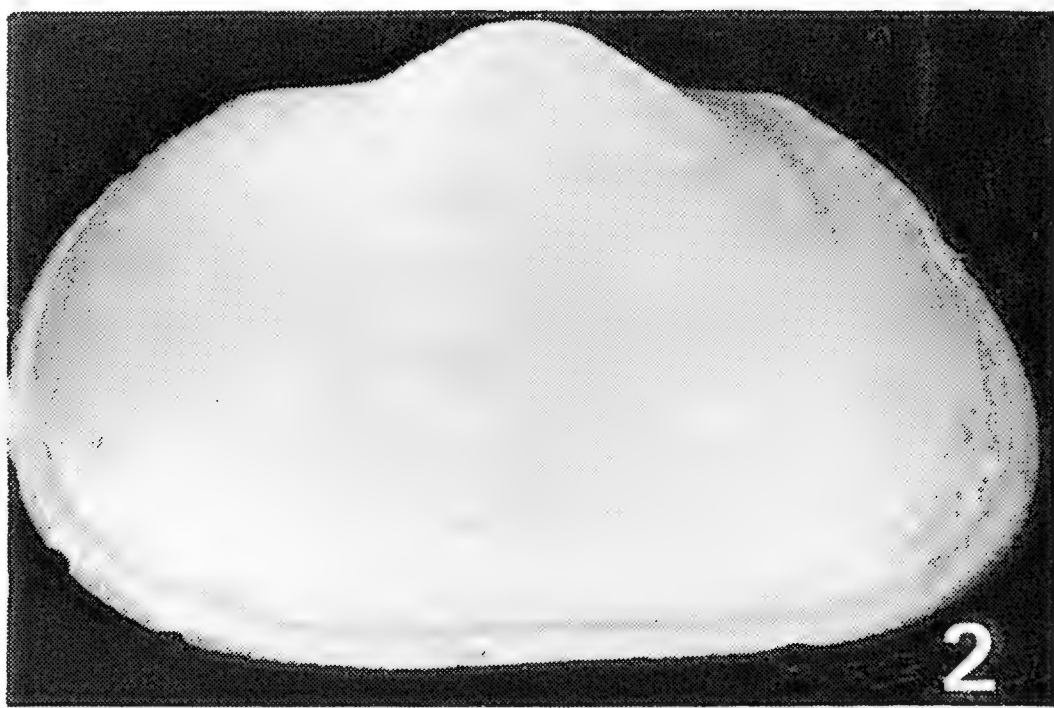
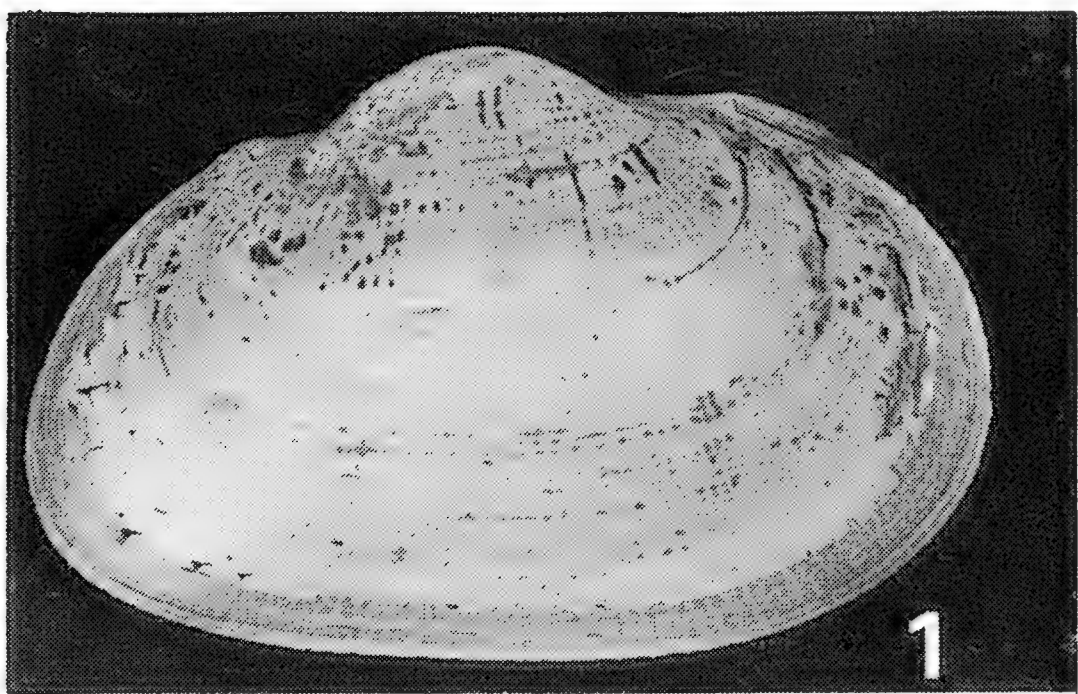
## PLATE 26 (opposite)

- Fig. 1. *Estellacar galactodes* from Foochow China; RV, periostracum removed; BM(NH). ×4.
- Fig. 2. *Estellacar saga*, Gladstone Harbour, Queensland; LV periostracum removed; AMS C140418. ×4.
- Fig. 3. *Estellacar galactodes*, Foochow, China; RV; BM(NH). ×4.3.
- Fig. 4. *Rectangularca africana*, Ameki, Nigeria, Eocene; B.M. Paleont. Dept. L48164. ×4.
- Fig. 5. *Estellacar olivacea*, Philippines; RV; NMW.1955.158. ×4.
- Fig. 6. *Rectangularca africana*, Ameki, Nigeria, Eocene; LV; BM Paleont. Dept. L48164. ×4.
- Fig. 7. *Estellacar olivacea*, Philippines; RV, periostracum removed; NMW.1955.158. ×3.5.
- Fig. 8. *Sanoarca* sp., Coon Creek, Tennessee; Upper Cretaceous; B.M. Paleont. Dept. ×6.

## PLATE 27 (overleaf)

- Fig. 1. *Estellacar galactodes* Foochow, China; LV with periostracum; BM(NH). ×4.
- Fig. 2. *Estellacar olivacea*, Philippines; LV with periostracum; NMW.1955.158. ×4.
- Fig. 3. *Scelidionarca pectunculiformis* Holotype, Borneo; LV with periostracum; BM(NH) 196257. ×2.6.
- Fig. 4. *Scelidionarca pectunculiformis* Holotype, Borneo; RV; BM(NH) 196257. ×2.
- Fig. 5. *Halonanus* cf. *pulchra*, Smithville, Texas; Eocene, LV; BM Paleont. Dept. L10151. ×4.3.







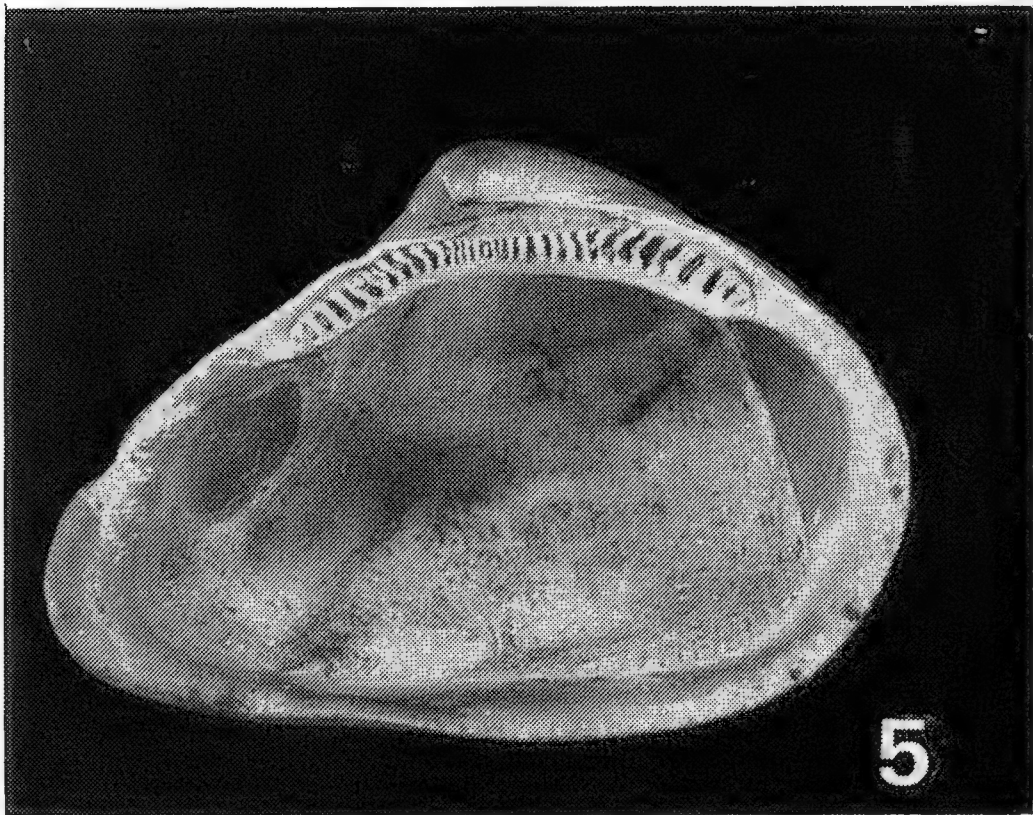
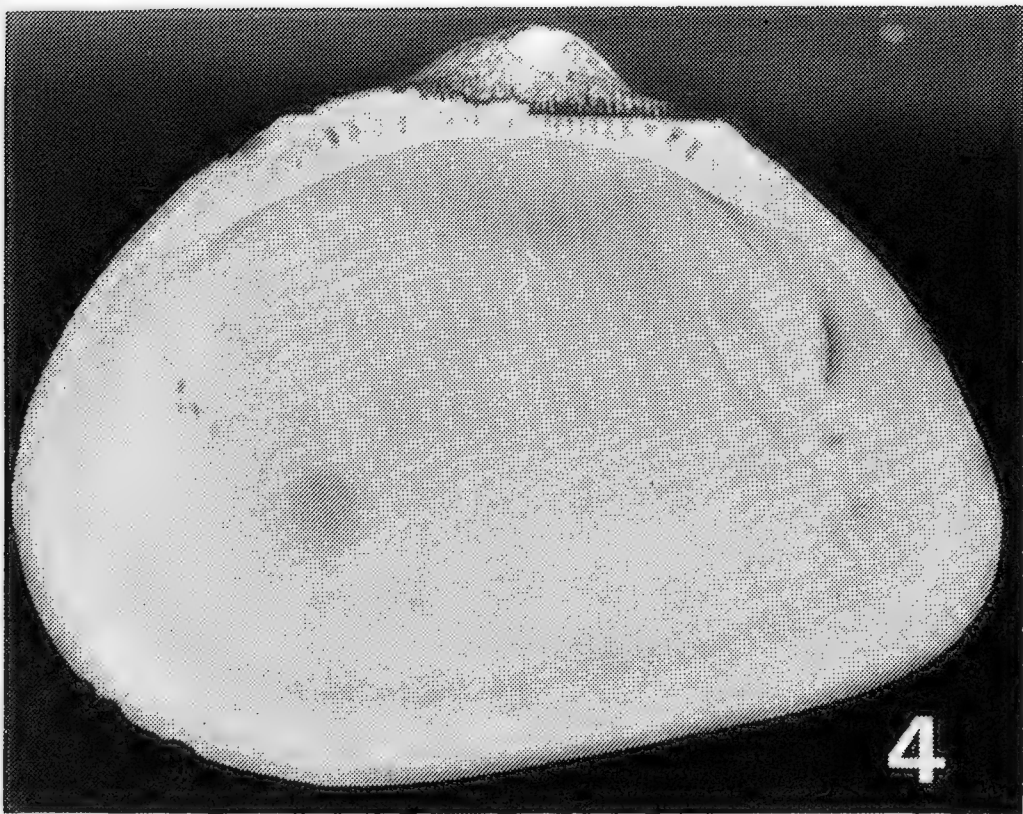
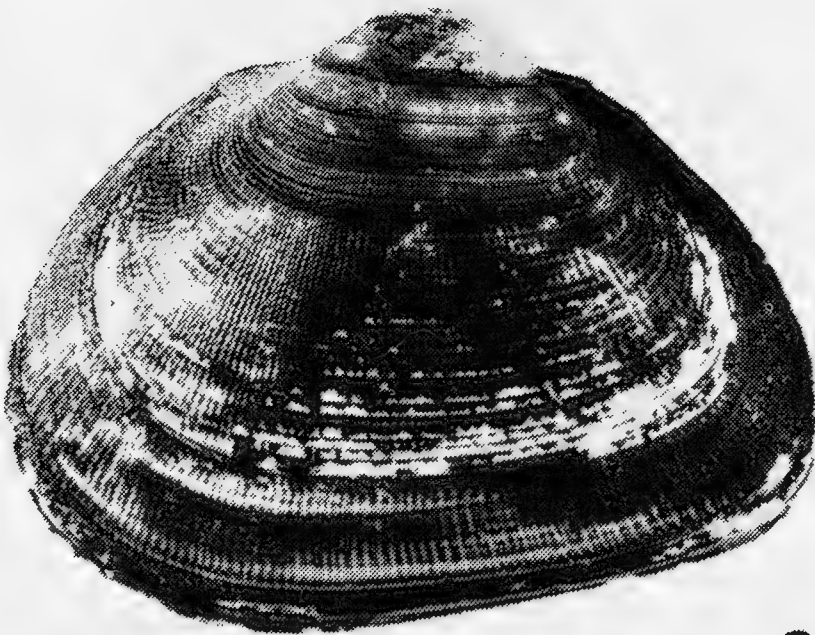
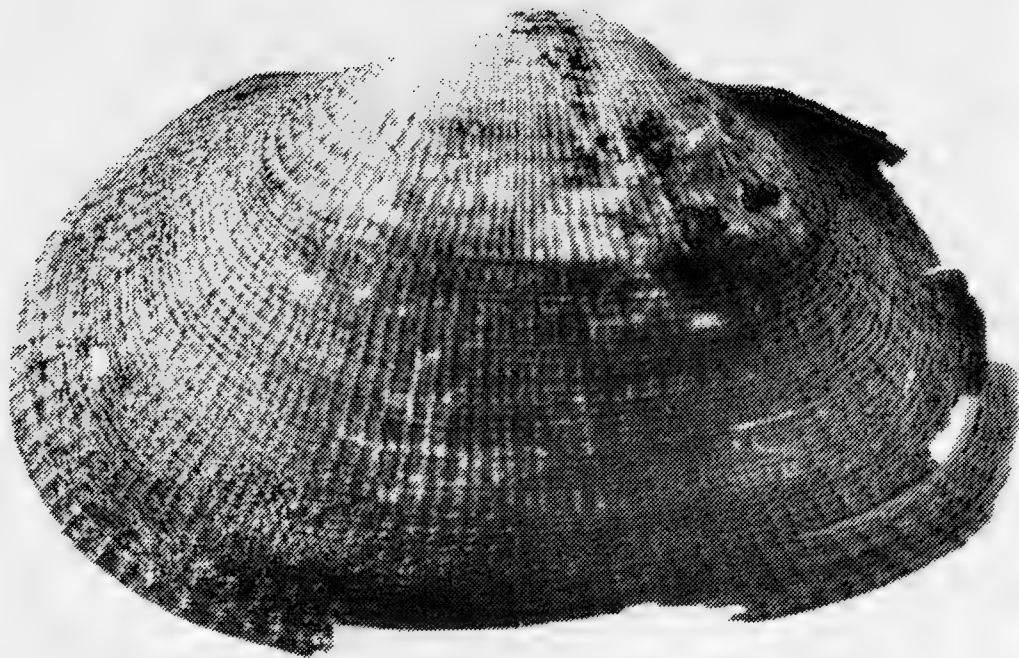


PLATE 27

# JOHN MORTON'S LIST OF NORTHAMPTONSHIRE MOLLUSCA (1712)

M. P. KERNEY<sup>1</sup>

(Accepted for publication, 19th April, 1986)

*Abstract:* A remarkable early 18th century list by the Reverend John Morton of over forty species of non-marine Mollusca, the earliest British 'local list', is republished and interpreted. Morton was the first to recognise a number of British species, including *Vallonia pulchella* (Müller), *Acanthinula aculeata* (Müller) and, probably, *Vertigo substriata* (Jeffreys).

The Reverend John Morton, M.A., F.R.S., was born in 1670 or 1671. He died on the 18 July 1726 at Great Oxendon, Northamptonshire, the parish which he had served, first as a curate and later as its rector, since 1701 (*Dictionary of National Biography*). A monument to his memory, erected at the expense of his friend Sir Hans Sloane, may be seen in the church. His enduring memorial is however his *Natural History of Northamptonshire*. Though published in the reign of Queen Anne, it is historically rather a product of the 17th century and of that short-lived flowering of interest in the natural world typified by such figures as John Ray, Robert Hooke, Martin Lister, John Woodward and Robert Plot – the last the author of the well-known *Natural History of Oxfordshire* (1676) and *Natural History of Staffordshire* (1686) which undoubtedly served as models for Morton's own book.

As in the works of Plot, a substantial part of Morton's folio is devoted to accounts of the rocks, minerals and fossils of the county. On fossils he held advanced views, rejecting the notions of Lister and Plot that they were created by a 'plastic virtue' and agreeing with Woodward that 'Tis as certain that *those* Shells are *real*: That they were once the Covers of Shell-fish, and their Origin at Sea, as that our Senses are capable of making a true Report of any thing whatever.' (p. 250). In addition to the Geology there are accounts of the plants and animals of the county, including – probably for the first time in a local work – an enumeration of the land and freshwater molluscs (*Exanguia Apoda*) 'to gratify those who are Curious in the History of these Elegant little Creatures . . .' (p. 415).

This extremely interesting list has not altogether received the attention it deserves. It was however reprinted in the late Victorian period (Morton 1885) with some annotations by J. W. Taylor and W. D. Roebuck attempting to translate Morton's nomenclature into Linnean terms. As recognised by those authors, there must remain a residue of doubt as to the identity of some of Morton's species. Nevertheless a careful scrutiny of his text and sources, amplified by the knowledge of present day molluscan distributions in the Midland counties, allows the present interpretation to be put forward with rather more confidence than was possible a century ago.

The species are set out below, using a modern taxonomy. Morton named his finds by consulting the works of Lister, usually his *Historia Animalium Angliae* (1678); these references are repeated here, without necessarily implying that his species were in every case the same as Lister's. A number of species Morton believed (not always rightly) to be 'wholly new and undescribed' and for these he furnishes descriptions and, in two cases, copper engravings (both reversed, for which he apologises; p. iii). His localities are here quoted verbatim; they are almost entirely in the north of the county, in the area around Great Oxendon (just south of Market Harborough) and extending eastwards along the valleys of the Welland,

<sup>1</sup> Department of Zoology, British Museum (Natural History), London SW7 5BD.



the Ise and the Nene to the margin of the Fens. National Grid references have been inserted where appropriate. Species for which no localities are given he regarded as common. A very few of Lister's species he thought were absent, notably *Theodoxus fluviatilis*, *Helix pomatia* (see below) and *Margaritifera margaritifera*; *Theodoxus* is a curious omission, as it is frequent today in the larger rivers.

In passing, it is worth noting that Morton was probably the first person to describe scientifically a Quaternary deposit containing land and freshwater molluscs. At Mears Ashby (SP 86) he dug a pit to examine the shell-bearing layers, which comprised a 'Moorish black Earth' overlying a tufa. He found five species, in modern nomenclature probably *Lymnaea truncatula* (Müller), *Succinea* or *Oxyloma* sp., *Cochlicopa lubrica* (Müller), *Trichia hispida* (L.) agg. and *Cepaea nemoralis* (L.) (Morton 1706; account repeated in Morton 1712, pp. 254–255).

## LIST OF SPECIES

The reference immediately following the species name is to Morton 1712.

**Viviparus** sp.; p. 417, line 21 (Lister 1678, Pl. 2, Fig. 18).<sup>1</sup> 'This sort we find in the *Weland* [Welland] and other of our Rivers, as also in the Fen-Ditches.'

**Pomatias elegans** (Müller); p. 415, line 15 (Lister 1678, Pl. 2, Fig. 5).

'not a very common one here; but yet under the Bushes by an old Stone-pit on the *South* Side of *Wakerly* Church [Wakerley, SP 9599]; and also under the Bushes upon a very steep Place of the *South* Bank of the *Weland* in *Wakerly* Lordship, there are many of them.'<sup>2</sup>

**Bithynia tentaculata** (L.); p. 417, line 9 (Lister 1678, Pl. 2, Fig. 19).

**Aplexa hypnorum** (L.); p. 418, line 29; Pl. 13, Fig. 2.<sup>3</sup>

'I first found it in some Ditches nigh Great *Bowdon* [SP 78] in *Leicestershire*, and since that as I remember in *Burrow-Fen* [Borough Fen, TF 20].'

**Physa fontinalis** (L.); p. 417, line 30 (Lister 1678, Pl. 2, Fig. 25).

'I have never met with them but in some few of our Fen-Ditches, and in that part of the *Ise* betwixt *Arthingworth* and *Newbottle* Bridge [SP 7681].'

**Lymnaea truncatula** (Müller); p. 418, line 23.<sup>4</sup>

'Tis found together with the former [*L. palustris*], and is almost as common.'

**Lymnaea palustris** (Müller); p. 417, line 23 (Lister 1678, Pl. 2, Fig. 22).<sup>5</sup>

'In the *Ise* below *Arthingworth* [SP 7681], and in the Fen-Ditches nigh Sir *John Shaw*'s Decoy [in Borough Fen near Peakirk, TF 2007].'

**Lymnaea stagnalis** (L.); p. 417, line 9 (Lister 1678, Pl. 2, Fig. 21).

**Lymnaea auricularia** (L.); p. 417, line 9 (Lister 1678, Pl. 2, Fig. 23).<sup>6</sup>

**Lymnaea peregra** (Müller); p. 418, line 13.<sup>6</sup>

'We find it in the Boggs and Brooks, as at *Arthingworth*: and 'tis no uncommon Shell.'

**Planorbis (Planorbis)** sp.; p. 417, line 9 (Lister 1678, Pl. 2, Fig. 27).<sup>7</sup>

**Anisus vortex** (L.); p. 417, line 35 (Lister 1678, Pl. 2, Fig. 28).<sup>8</sup>

'In the *Ise* and other of our Brooks, as also in the Fens.'

**Planorbarius corneus** (L.); p. 417, line 9 (Lister 1678, Pl. 2, Fig. 26).

**Ancylus fluviatilis** Müller; p. 417, line 37 (Lister 1678, Pl. 2, Fig. 32).

'I found a great Number of them affix'd to loose Stones lying in the Water underneath a small Bridge [SP 9592] in the Lane that leads up to *Dean* [Deene] from *Dean-Thorp* [Deenethorpe].'

**Succinea putris** (L.); p. 417, line 26 (Lister 1678, Pl. 2, Fig. 24).

'In our larger and older Pools in Plenty . . .'

(?) **Oxyloma pfeifferi** (Rossmässler); p. 417, line 27.<sup>9</sup>

'in the Boggs in the Clayland.'

**Cochlicopa lubrica** (Müller); p. 415, line 23 (Lister 1678, Pl. 2, Fig. 7).

'occurs very frequently in all our moister Woods, in the Moss at the Roots of the old trees; as also among the Moss and Sedge upon the Boggy Sides of several standing Springs, as at *Oxendon* [SP 78] and *Arthingworth* [SP 78].'

**Lauria cylindracea** (da Costa); p. 415, line 20 (Lister 1678, Pl. 2, Fig. 6).

'found in great plenty in a Ground nigh *Morsley* Wood [Mawsley Wood, SP 7976], especially upon a Stone-Heap there.'

**Vallonia pulchella** (Müller); p. 417, line 1.<sup>10</sup>

'I have found it in Boggy Places in *Oxendon* and *Arthingworth* Fields in great Plenty.'

**Acanthinula aculeata** (Müller); p. 415, line 39.<sup>11</sup>

'in *Morsley* Wood; but 'tis extremely rare.'

(?) **Vertigo substriata** (Jeffreys); p. 416, line 17.<sup>12</sup>

'I found it in the Clefts of a Sallow-Root, in a Thicket of Sallows near a Pond of Mr. *Chamberlain's*, in *Thorpe Mandeville* Lordship [Thorpe Mandeville, SP 54; possibly SP 5345].'

**Ena obscura** (Müller); p. 415, line 28 (Lister 1678, Pl. 2, Fig. 8).<sup>13</sup>

'with [*Cochlicopa lubrica*] in the same Woods, but much more rarely.'

**Discus rotundatus** (Müller); p. 416, line 40.<sup>14</sup>

'We find it in a little Wood call'd *Loteland* [Loatland, SP 7782], nigh *Harrington*, amongst the Moss at the Roots of the Ashes and Oaks, and in many other of our Woods.'

**Arion ater** (L.); p. 414, line 42 (Lister 1678, Pl. 2, Fig. 17).

**Oxychilus** sp. or **Aegopinella** sp.; p. 416, line 34.<sup>15</sup>

Described as a 'Wood' species.

**Limax maximus** L.; p. 414, line 42 (Lister 1678, Pl. 2, Fig. 15).

**Deroceras reticulatum** (Müller); p. 414, line 42 (Lister 1678, Pl. 2, Fig. 16).

**Cochlodina laminata** (Montagu); p. 415, line 32.<sup>16</sup>

Found with the next species (*C. bidentata*) 'tho' more rarely, in the same Woods.'

**Clausilia bidentata** (Ström); p. 415, line 31 (Lister 1678, Pl. 2, Fig. 10).

'in the Woods at *Cliff* [Cliffe, SP 9997], and in many others . . .'

**Balea perversa** (L.); p. 416, line 4; Pl. 13, Fig. 1.<sup>17</sup>

'I first found it in 1695. in a Wood that had been new cut down at *Morsley* [Mawsley, SP 8076]: and since not unfrequently in the thicker Parts of the Neighbouring Woods amongst Moss.'

**Helicella itala** (L.); p. 415, line 9 (Lister 1678, Pl. 2, Fig. 13).

**Trichia striolata** (C. Pfeiffer); p. 415, line 43 (Lister 1678, Pl. 2, Fig. 12).<sup>18</sup>



**Trichia hispida** (L.) agg.; p. 416, line 26.<sup>19</sup>

'Tis not unfrequent in our Woods, particularly in those about *King's-Cliff* [King's Cliffe, SP 9997].'

**Arianta arbustorum** (L.); p. 415, line 9 (Lister 1678, Pl. 2, Fig. 4).

**Helicigona lapicida** (L.); p. 415, line 46 (Lister 1678, Pl. 2, Fig. 14).

'in Hedge-Bottoms on the *West Side of Oakly parva* [Little Oakley, SP 8985], by the Road to *Stanian* [Stanion].'<sup>20</sup>

**Cepaea nemoralis** (L.); p. 415, line 9 (Lister 1678, Pl. 2, Fig. 3).

**Helix aspersa** Müller; p. 415, line 9 (Lister 1678, Pl. 2, Fig. 2).

[**Helix pomatia** L.; p. 415, line 1 (Lister 1678, Pl. 2, Fig. 1).

'The Great Edible Snail, tho' common in some Places in the *Southern Parts of England*, yet can scarce be brought to live with us; as appears by an Experiment made by the late Lord *Hatton*, who put a great many live ones of this Kind into a convenient Coppice near his House at *Kirby* [Kirby Hall, SP 9292], with Intentions that they should breed there; but in a short time they all dy'd.'<sup>21</sup>

**Unio pictorum** (L.); p. 418, line 6 (Lister 1678, Pl. 2, Fig. 30).

'in the River *Nyne* [Nene] near the Influx of the *Ise* [SP 9067].'

**Anodonta cygnea** (L.); p. 417, line 45 (Lister 1685, p. 9; 1685–92, Pl. 156).

'We have it in some of our old Ponds, as in those of Sir *John Langham's* at *Cosbrook* [Cottesbrooke Hall, SP 7173].'

**Anodonta anatina** (L.); p. 418, line 3 (Lister 1685, Fig. 2; 1685–92, Pl. 153).

'In the *Ise*, the *Nyne*, and indeed all our other Rivers.'

**Sphaerium corneum** (L.); p. 417, line 41 (Lister 1678, Pl. 2, Fig. 31; 1685–92, Pl. 159).<sup>22</sup>

'It occurs very frequently in our Ponds and Brooks.'

**Pisidium** spp.; p. 418, line 38.<sup>23</sup>

'There are plenty of them in the Boggs in *Arthingworth* and *Oxendon* Fields. Also in the *Ise*, and I suppose in other of our Rivulets.'

#### NOTES

- 1 Lister's figure of 1678 is probably intended to represent *V. contectus* (Millet) rather than *V. viviparus* (L.). Nevertheless it is unlikely that he or Morton distinguished between these species, both of which occur in the Welland.
- 2 This snail is extremely local in the east Midlands and is almost extinct in Northamptonshire. At the first place mentioned by Morton, an old stone quarry just south of Wakerley church (SP 958990), it was rediscovered by Mr Frank A. Adams in 1969, still flourishing. It lives also in Wakerley Great Wood nearby (SP 967985).
- 3 Morton regarded this as a new species, which he described and illustrated. He was evidently unaware of the illustration in Lister's *Historia Conchyliorum* (2nd issue, supplementary Pl. 1059, Fig. 5) of a shell collected by James Petiver at Mitcham in Surrey.
- 4 Described as a new species: 'tis much like [*Lymnaea palustris*] . . . But 'tis smaller by more than one half, and its Wreaths are somewhat more Prominent or Tumid.' This appears to be the first British record of the species.

- 5 Some authors (e.g., Gray 1840, p. 48) have taken Lister's figure 22 to represent *Lymnaea peregra* (Müller). Müller (1774, p. 131) and Montagu (1803, p. 370) believed it to be *L. palustris* and this interpretation seems unequivocal from a reading of Lister's text (p. 139), including his reference to the species being frequent in swamps ('stagnis').
- 6 Though Lister's description of his '*Buccinum pellucidum, subflavum . . .*' (1678, p. 139) seems to refer at least in part to *Lymnaea peregra*, his engraving (fig. 23) was probably taken from an example of *L. auricularia*. This evidently confused Morton, who carefully describes what must be *L. peregra* as a new, distinct species, common in his own area. By implication *L. auricularia* was known to him also.
- 7 Neither Lister nor Morton are likely to have distinguished *P. planorbis* (L.) from *P. carinatus* Müller. Müller himself (1774, p. 157) interpreted Lister's drawing as being of his own species, though most subsequent authors have favoured *P. planorbis*. Both species occur in Morton's area.
- 8 Lister's figure and accompanying description (p. 145) could refer either to *A. vortex* or to *A. leucostoma* (Millet). Morton's river habitats are more compatible with the former.
- 9 Morton gives this as a variety of *Succinea putris*: 'But for the most part much smaller . . . ; so that I suspect them to be of a different Species.'
- 10 Vividly described by Morton as a new species ('A compressed umbilicated *Cochlea*, the smallest of all the Kind, of only Three Wreaths, with a round Aperture whose Margin is bended a little backward.') This is the first British record of the genus. Though Kennard and Woodward (1926, p. 138) suggest this is *V. excentrica* Sterki, the marsh habitat makes identification with the present species almost certain.
- 11 Morton took this to be a variety of *Euconulus fulvus* (Lister 1678, p. 123), but 'the Doctor's has (as he says) Six or Seven Circles or Wreaths, this no more than Five at the most, and the live Shell is all over a little brisly.' This is the first British record of the species.
- 12 Morton's description runs as follows:

'*Trochilus exiguus 4 spirarum elegantissime striatus.*' 'Tis a very small Shell, scarce the Fourth Part of a Barley Corn in Bigness, the Colour a lighter Brown, of the *Trochus* Shape, having Four Wreaths fashioned, as those of the *Trochi marini*, with a pretty flat Basis. 'Tis very neatly streak'd or striated with deep *Striae* transversly to the Turn of the Wreaths. The larger Wreaths rise up into a sharpish Ridge.'

The identity of this shell has given rise to some debate. Jeffreys (1830, p. 332) synonymised it with his new species *Helix mortoni*, from 'the rejectamenta of the Avon river, near Bristol'; this Gray (1840, p. 148) and later Jeffreys himself (1862, p. 171) regarded as only a depressed variety of *Euconulus fulvus* (Müller). Turton (1831, p. 44) thought Morton's snail was *Acanthinula aculeata*. Taylor and Roebuck (in Morton 1885, p. 321) suggest 'it may possibly be *Helix pygmaea* [*Punctum pygmaeum* (Draparnaud)], but is more likely to be young *H. rotundata* [*Discus rotundatus*].' Lastly, through an odd chain of events, it was confused with the mediterranean xerophile *Trochoidea elegans* (Gmelin). The circumstances behind this are briefly as follows. Pennant (1777, p. 127; pl. 80, fig. 108) described (very poorly) under the name *Trochus terrestris* a new British species from Cumberland, possibly based on *Euconulus fulvus*. Da Costa (1778, pp. 35–36) proposed two varieties of this: *Listeri* and *Mortoni*, the latter for the reception of Morton's striated Northamptonshire shell, the description of which he repeats almost verbatim. Montagu (1803, p. 287 & p. 427) accepted the former as identical with his new species *Helix trochiformis* (= *Euconulus fulvus*) but was clearly puzzled by the latter; he had seen no British specimens and describes in its place what is evidently the continental *Trochoidea elegans*, stating 'There can be little doubt but this is the same as that found by MORTON in Northamptonshire . . .' This confusion was repeated by later authors and as recently as 1951 resulted in *T. elegans* being listed as a Census record for vice-county 32, albeit as an old record requiring confirmation (Ellis 1951, p. 192)!

The identity of Morton's find with *Vertigo substriata* has not previously been suggested. His description recalls an immature pupillid or vertiginid – trochiform and not cylindrical at the 3 to 4 whorl stage. The fact that the shell was deeply and 'very neatly' striated agrees with the most distinctive feature of *V. substriata*: its well defined and very regular sculpture, just apparent to the naked eye and immediately obvious under a simple lens, particularly in juveniles when the periostracum is fresh and unabraded. The light brown colour and minute size are also compatible with such an identification. The habitat – a marshy *Salix* wood – is a characteristic one. Altogether it seems highly likely that Morton had recognised this snail in Northamptonshire over a century before its rediscovery in the north of England in the 1820s.

*Vertigo substriata* must be accounted a rare species in lowland England, though surviving sporadically in most counties in a few undisturbed marshy places. There are several old finds from Northamptonshire (e.g., from a willow marsh at Haselbech (SP 77); Shaw 1905). The site at Thorpe Mandeville deserves to be revisited, if it still exists.

- 13 Taylor and Roebuck (*in* Morton 1885) thought this to be probably *Azeca goodalli* (Férussac). Lister's figure is poor but his description (p. 122) clearly refers to *Ena obscura*.
- 14 Regarded as new, and identified by a detailed description. Morton overlooked Lister's engraving of the same species in *Historia Conchyliorum* (2nd issue, supplementary pl. 1058, fig. 11).
- 15 Morton's description could apply to several of the larger zonitids, such as *Oxychilus cellarius* (Müller) or *Aegopinella nitidula* (Draparnaud).
- 16 Described by Morton as 'a larger Variety' of *Clausilia bidentata*.
- 17 Lister had earlier described *Balea perversa*, which he had found in Cambridgeshire on the trunks of old ash trees (1678, p. 124; pl. 2, fig. 11). Morton however thought that his 'own find was of a different, hitherto undescribed snail, as it appeared to be smaller, and to lack the basal angulation which is suggested by Lister's description and poor engraving; in Morton's words, 'Neither is there drawn around the Middle of its Basis or First Wreath, a sharp Ridge, as in that.' In his own engraving he indeed shows 'a roundish Mouth', making it certain that what he had was *Balea* and not juvenile *Clausilia*.

*Balea perversa* is today rare in the Midland counties, probably through atmospheric pollution (Holyoak 1978). In this part of Northamptonshire it has not been recorded for about a hundred years (e.g., Castle Ashby (SP 85), 1879; wall near Moulton Park (SP 76), 1883).

- 18 Lister's figure probably represents his variety found in Kent (= *Monacha cantiana* (Montagu)) rather than the species to which his main description (p. 125) evidently refers. Morton's woodland habitats nevertheless imply *T. striolata*.
- 19 Described by Morton as 'beset all over with short and stiff little Hairs or Bristles.' He recognised the same species as a fossil in the Postglacial deposit at Mears Ashby, and that it had probably 'not hitherto been mention'd by any Writer; tho common enough in the Woods with us . . .' (p. 255). Since *Trichia plebeia* (Draparnaud) virtually replaces typical *T. hispida* in this area Morton's shell is probably the former.
- 20 Not refound recently in this area, and perhaps locally extinct.
- 21 Scattered colonies of *Helix pomatia* reported from this part of Northamptonshire during the past century (Woodford, Sudborough, Rockingham, etc.) may have originated as introductions of this kind.
- 22 The identity of the shells figured by Lister is uncertain. Fig. 31 (1678) may well be *Sphaerium lacustre* (Müller), while the illustration in *Historia Conchyliorum* (pl. 159) could refer to *S. rivicola* (Lamarck).

- 23 Described as new, and 'of several Sizes, from that of a *Lettice* to that of a *Hemp-seed*.' Those in boggy ground were no doubt *P. personatum* Malm or *P. casertanum* (Poli). This appears to be the first British record of the genus.

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# CALYPTRAEA CHINENSIS (MOLLUSCA, GASTROPODA) ON THE WEST COAST OF IRELAND: A CASE OF ACCIDENTAL INTRODUCTION?

DAN MINCHIN<sup>1</sup>, DAVID McGRATH<sup>2</sup> AND COLM B. DUGGAN<sup>1</sup>

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**Abstract:** The Chinaman's hat shell, *Calyptrea chinensis* (L.) has been taken in abundance in Clew Bay and Ballynakill Harbour on the west coast of Ireland in recent years. Both of these areas were surveyed extensively in the late 19th and early 20th centuries. *C. chinensis* was not recorded from these areas at that time. Other records of the species from Irish waters are restricted to east and south west coasts, and date from the last century. It is suggested that the recent records result from an introduction of this species with relaid oysters which originated from the French coast.

## INTRODUCTION

In this account the present distribution of the *C. chinensis* population on the west coast of Ireland is documented and the possible origin of this species is discussed.

## OBSERVATIONS

**Clew Bay:** In 1963, one of us (CBD), in an unpublished report, noted the occurrence of *C. chinensis* in one area of Clew Bay during a survey of oyster beds. Sixty three stations in the vicinity of Quinsheen Island were sampled by 0.21 m<sup>2</sup> van Veen grab and seven specimens taken. None were taken at that time in Inishlyre Harbour (Fig. 1) where 78 stations were sampled by grab, and 7 dredge hauls were made. During the years 1980–81, a total of 121 dredge hauls were carried out in the channels between the drumlins of the inner bay and some hundreds of *C. chinensis* collected. Specimens were found throughout the area from Annagh Island north to Inishcuill, and noted as common in the area bounded by Inishlyre Harbour, Collan More and Inishraher. They were plentiful, more than 10 per haul, in dredgings between Inishraher and Carraignamore. Up to seven specimens were taken on a single valve of the clam, *Venerupis pullastra* (Montagu) in the channel SE of Collan More. Individuals were found attached to stones, rocks and the shell debris of various bivalve species, including *Ostrea edulis* L., and also on live oyster shells. Smaller *C. chinensis* were also found on the shells of larger individuals. Specimens were taken most frequently on the inner surface of single and paired bivalve valves, particularly those of *Ensis* and oysters. *Calyptrea* were taken in the southern region of Newport Bay, to as far North as Inishloy (Fig. 1) where a single specimen was captured on 3 November 1983 in three 5 minute dredge hauls.

**Ballynakill Harbour:** Specimens were noted as common on small stones around low water spring tide mark, on the shore between the SE tip of Coastguard Bay and Ross Point, on

<sup>1</sup> Fisheries Research Centre, Department of Fisheries and Forestry, Abbotstown, Dublin 15, Ireland.

<sup>2</sup> Department of Zoology, University College, Galway, Ireland.

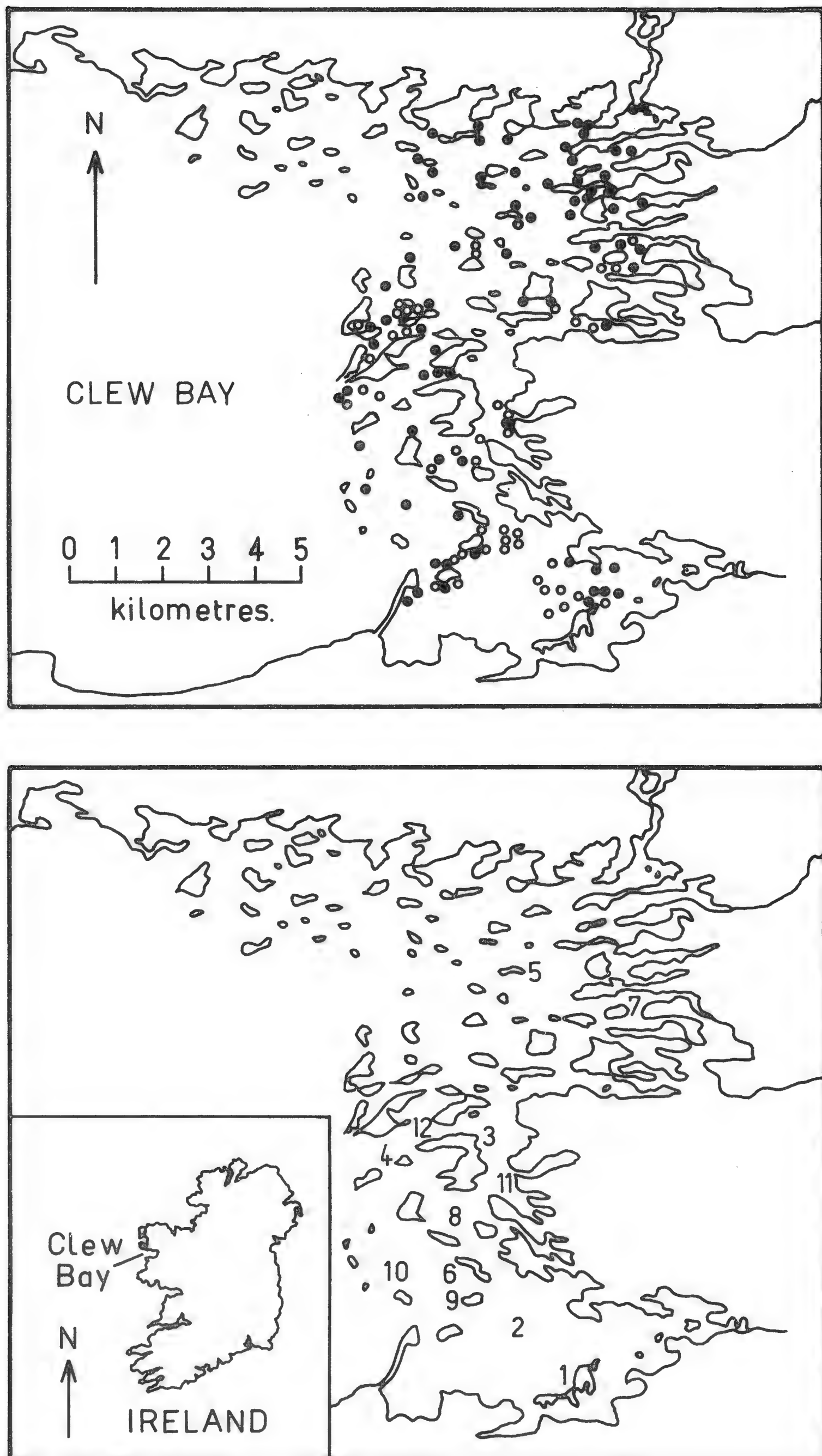


Fig. 1. Distribution of *Calyptrea chinensis* (open circles) in Clew Bay during 1980–83 with some records from 1963, and areas where it was absent (dots). Places mentioned in the text are:  
 1. Annagh Island 2. Carraignamore 3. Collan More 4. Collanbeg 5. Inishcuill 6. Inishgowla 7. Inishloy 8. Inishlyre Roads 9. Inishraher 10. Inishimmel 11. Rossmindle 12. Quinsheen.

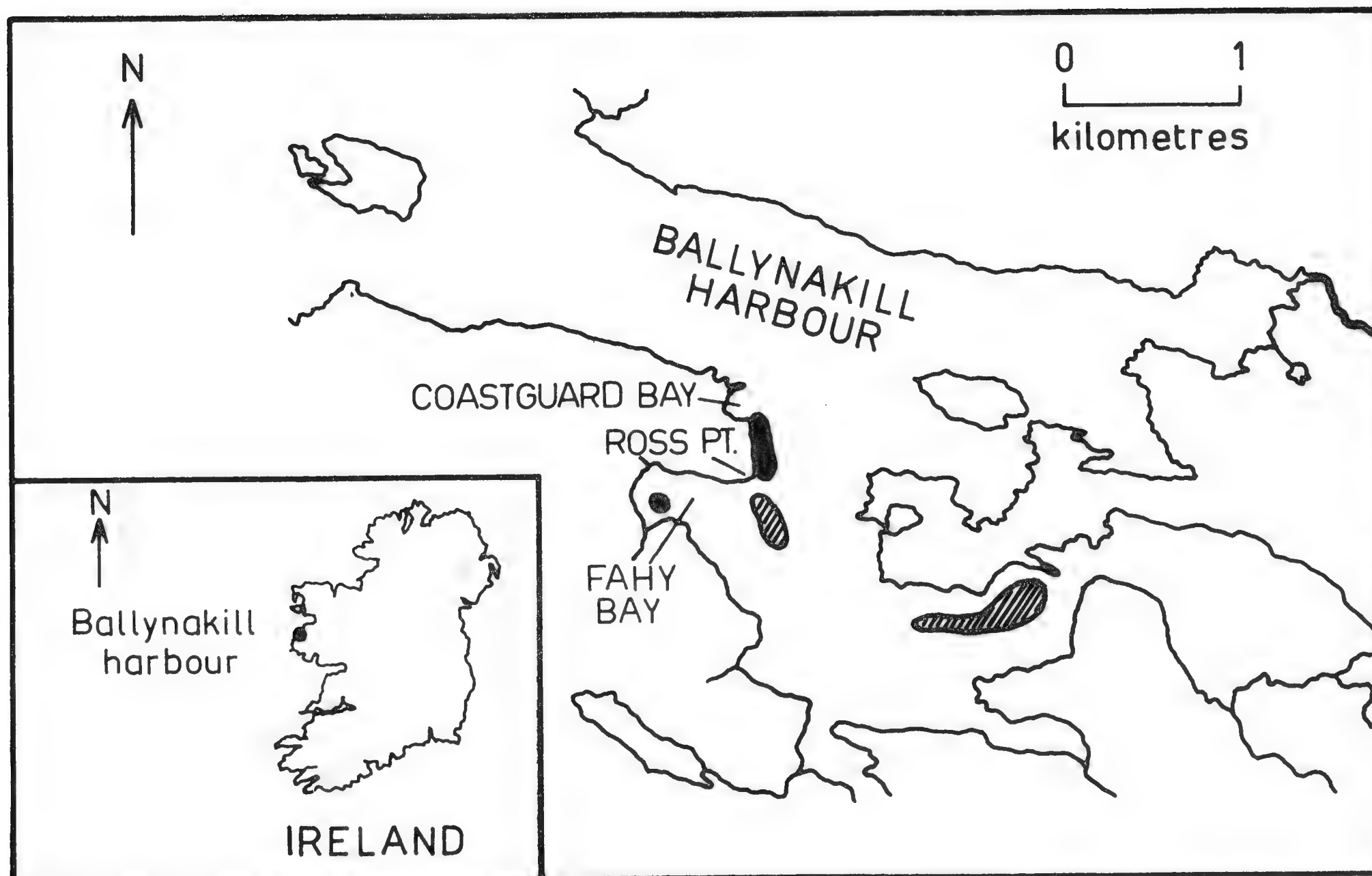


Fig. 2. Distribution of *C. chinensis* in Ballinakill Bay from records collected during 1980 and 1982 (black), and where not found (hatched).

15th May, 1980 (Fig. 1). A single dead shell had been found in the area previously, in 1975, by Dr. Brendan O'Sullivan. In July 1982, four (11–16 mm length) were found attached to an *Ensis* shell at 3 m depth at the western end of Fahy Bay, close to the submerged wreck of the old floating laboratory used by Sykes at the turn of the century (Sykes 1905).

There are records of *C. chinensis* in Irish waters in the 19th century from the east and south-west coasts of Ireland. However, Turton's (1819) record from Dublin Bay is regarded by Jeffreys (1865) as 'probably erroneous'. Both Jeffreys (1869) and Nichols (1900) cite a record of the species from Dublin Bay giving McCalla as the authority, and Nichols (1900) also refers to specimens, still extant, labelled 'Dublin Bay' in the collections of the National Museum of Ireland. D'Alton (1838) refers to oysters from Arklow being relaid in the Sutton bed in Dublin Bay and later reports (Anon 1883, 1892) indicate that relayings of French oysters also took place, but all these records are later than Turton's (1819).

Thompson (1856) lists *C. chinensis* from 'the east coast'. However Nichols (1900), without explanation, describes the east coast records as 'doubtful', Wright and Greene (1859) and Bourne (1890) record specimens from deep water off the SW coast, the latter noting several individuals from 128 m depth. Transfers from deep water off the SW coast to the shallow waters of Clew Bay and Ballinakill Bay either on oysters (which are not known to occur in deep water in this area) or on their own, are unlikely. The authors do not know of any other recent Irish records of this species. It has not been recorded in the Galway Bay area despite extensive collecting in recent years, nor was it recorded to the north of Clew Bay in the area about Blacksod Bay (last survey, October 1983 by CBD) and the Mullet Peninsula (Farran 1915, Hayward 1972).

The populations recorded in this account in Clew Bay lie within the area studied during the Clare Island survey. During the period 1909–1911, extensive intertidal and sublittoral sampling was carried out in the Clew Bay area by a group of distinguished naturalists in an



interdisciplinary research programme organised by R. L. Praeger. In his account of the marine Mollusca, Colgan (1911) lists fifty two effective dredge hauls, of which twenty nine were from shallow water. These latter were concentrated on the neighbourhood of Clare Island and Westport Bay and channel. Dredges were taken in the inner bay area as follows:

May, 1909	Inishlyre Roads, (Harbour) five fathoms, at anchorage.
July, 1909	Inner islands of bay from Rossmindle to Sruhnamel (Maelstrom), round Inishlyre and Collanbeg, four hauls, 2–5 fathoms.
August, 1909	Inishgowla, 4 fathoms.
May, 1910	Twelve hauls in Westport Channel (nine off Scotch bonnet and Innishimmel, and three in Inishlyre Roads (Harbour).
August, 1910	Inishlyre Roads, two dredges, 2, 4 fathoms.

Colgan (1911) lists two hundred and forty seven species of marine Mollusca from the Clare Island survey, but does not include *C. chinensis*.

During the period 1894–1914, at various times, a floating marine laboratory was moored in Fahy Bay, Ballynakill Harbour. The results obtained and the collections made during this period were made available to augment the work done during the Clare Island survey (Southern 1915). The greater part of the shore collecting in Ballynakill Harbour was done in the section from south of Coastguard Bay to Sligagh, within which the *C. chinensis* was noted as common in 1980. *C. chinensis* is not listed in Southern (1915) or any part of the area considered by him, including Ballynakill Harbour.

An earlier survey in Ballynakill Harbour conducted by Sykes (1905) from the floating laboratory moored in Fahy Bay does not list the species either. It seems very unlikely that, had *C. chinensis* been present in the area at the turn of the century, such a conspicuous and unmistakable species would have been overlooked. Furthermore, no evidence is available to suggest that any transfers of molluscs or seabed material have taken place within Ireland from areas where *C. chinensis* is known to have occurred. In Britain *C. chinensis* is recorded from the southwest, the Isle of Man, and Loch Ryan in the Clyde (McMillan 1968, Seaward 1979). It has been suggested that the population in Loch Ryan was introduced with oysters from Brittany (Allen 1962, McMillan 1968), where *C. chinensis* is common, at a time when oysters were being introduced throughout west Scotland. Official records held in the Department of Fisheries and Forestry show that introductions of oysters have been made to the Clew Bay area as follows:

1906–1910	613,000 French oysters at Inishlyre Harbour.
1934	16,500 Dutch oysters at Inishlyre Harbour.
1937	38,500 at Quinsheen – origin not known.
1940	30,000 from Brittany at Inishlyre harbour.
1949–1954	500,000 from Brittany, at Quinsheen.

Oysters were imported from Brittany and laid in Ballynakill Harbour during the 1950s and 1960s. Because of shell disease in France, Ireland did not permit any importations of French oysters after 1965.

The evidence available suggests that *C. chinensis* were absent from both Clew Bay and Ballynakill Harbour at the turn of the century. The fact that specimens were found only at Quinsheen in 1963 suggests that the species was introduced to that area shortly before i.e. from Brittany in the period 1949–54. Their absence from Inishlyre Harbour in 1963 suggests that they were not introduced with the French oysters planted there in 1906–10 nor with Dutch oysters laid in 1934. Korringa (1951) in his extensive study on the epifauna of oyster shells did not find *C. chinensis* on Dutch oysters.

Commercial dredging for oysters resumed in Clew Bay in the late 1970's having ceased in the late 19th or early 20th century. This activity must assist the spread of *C. chinensis*,

which, having no planktonic larval stage is otherwise restricted in its dispersal to pedal movement or movement of substrate to which it is attached, particularly when dredged material is brought aboard a moving boat and dumped elsewhere. French oysters were also laid in Tralee Bay, in 1936, but no *C. chinensis* have been found there. It may be expected, due to the reopening of commercial fishing for oysters in Clew Bay, that *Calyptraea* will extend further northwards into Newport Bay and will spread to other localities by the relaying of Clew Bay/Ballynakill oysters. Fortunately this species does not pose any problems for oyster cultivation, unlike the closely related *Crepidula fornicata* (L). Material collected from Westport Bay on 8 June 1980 has been deposited in the Irish National Museum (NMI 42–1981).

#### ACKNOWLEDGEMENTS

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## COMMUNICATIONS

### *TANDONIA RUSTICA* (MILLET), A SLUG NEW TO THE BRITISH ISLES

On 22 June 1986 I was collecting molluscs and other invertebrates in an area of old woodland on the limestones of the Hythe Beds (Lower Cretaceous) at One Tree Hill (51/5653), near Sevenoaks in West Kent. The area was rich in molluscs and species such as *Cochlodina laminata* (Montagu), *Macrogastra rolphii* (Turton) and *Clausilia bidentata* (Ström) were recorded. Tree felling had been taking place as part of the normal woodland management and the many logs lying on the ground provided ideal resting sites for invertebrates. On turning over one such log I immediately spotted a strange slug that looked exactly like the illustration of *Milax rusticus* on plate 12 of Kerney & Cameron's *Field Guide* (1979). On further examination it compared favourably with the description in that book, being of a very pale dirty white with a reddish flush and well spotted in black. The keel was pale and the sole yellowish-white. The mucus was colourless and very sticky.

*Tandonia rustica* is a central and southern European species found in the wilder, less cultivated areas, particularly in woods and open waste ground. It favours calcareous soils. It is known from Austria, Belgium, Bulgaria, Czechoslovakia, France, Germany, Holland, Italy (including Sicily), Poland, Spain, Switzerland and Yugoslavia (Dalmatia). The habitat at One Tree Hill is in keeping with the normal habitat of the species and suggests a relic population rather than a recent introduction. A further search failed to produce any more specimens but the following other species of slugs were noted: *Arion ater* (L.) s.s., *A. subfuscus* (Draparnaud), *A. fasciatus* (Nilsson), *A. distinctus* Mabile, *Limax maximus* L. and *L. marginatus* Müller.

I would like to thank Adrian Norris for confirming the identification of this slug and for much useful information. He informs me that the correct generic name for this species should now be *Tandonia* rather than *Milax* sensu stricto (see also Wiktor, *Malak. Abh. Mus. Tierk. Dresden* 7 (1981), p. 145).

ERIC G. PHILP

Maidstone Museums & Art Gallery, St. Faith's Street, Maidstone, Kent ME14 1LH

(Received, 18 September 1986)

### THE IDENTITY OF *HELICELLA* (*LEJEANIA*) *CHIONOBASIS* PILSBRY

Whilst recently attempting to identify a helicid from Ethiopia my attention was drawn once again to all the published descriptions of species from NE. Africa purporting to belong to the group. These are mostly listed by Bacci (*Ann. Mus. Civ. Stor. nat. Giacomo Doria* 65 (1951), pp. 93–96) but he omitted the species described by Pilsbry, although he cites the paper concerned in his bibliography.

In 1894 the American Dr. A. Donaldson Smith made an extended journey in NE. Africa and collected both plants and animals. From his collection H. A. Pilsbry described *Helicella* (*Lejeania*) *chionobasis* in 1897 (*Proc. Acad. nat. Sci. Philad.* 49 (1897), p. 359) and the identity of this has intrigued me for over 20 years. Through the kindness of Dr. G. M. Davies I have been able to examine the holotype (and presumably only specimen); even before completely unpacked I could see at a glance it was a *Trochonanina* of the *Bloyetia* group and not a helicid at all. The mystery was partly solved but the group, as I have previously pointed out (*Rev. Zool. Bot. afric.* 71 (1960), pp. 241–245), needs thorough revision. Under the present circumstances I am merely transferring it to the correct genus.

*Trochonanina* (*Bloyetia*) *chionobasis* (Pilsbry, 1897).

*Helicella* (*Lejeania*) *chionobasis* Pilsbry in *Proc. Acad. nat. sci. Philad.* 49, p. 359 (1897).

SOMALI REPUBLIC (N.). The Haud, 25 July 1894, leg. A. Donaldson Smith in ANSP 68116 (holotype).

The Haud is the name given to an extensive area of the south-western plateau area of the Northern Region of the Somali Republic and the adjoining area of the Ethiopian Ogaden. Haud-type mixed bushland extends southwards through the Ogaden into the Northern Province of Kenya (Hemming, *Proc. Linn. Soc. Lond.* 177 (1966), p. 221). A map of Donaldson Smith's journey is given in the *Geographical Journal* (16(1900), p. 712) and an account of his travels in his own book (1897), *Through unknown African countries* (London and New York). He left Berbera on the 10th July 1894 and arrived in Hargeisa on the 17th where he stayed for several days. From there to Mil Mil in the Ogaden was about 100 miles across the fairly cool Haud Plateau at 1650 m. On the 27th July he was at Gagep on the Tug Mil Mil and on the 25th he was presumably a little to the north near the southern edge of the Haud. It is not possible to be more precise and I have seen no other specimens from this area.

The shell is thick, the initial two whorls deep indigo, almost black, and the next whorl paler but still dark-coloured with some plicae white; the rest of the upper surface is brown with many of the coarse plicae white; the under surface is chalky white. I am afraid the great man of malacology is not really to be forgiven since although

## COMMUNICATIONS

the protoconch shows fine but distinct transverse striae and there are only the slightest traces of a spiral element, the base of the shell has the typical wavy spiral striae present in so many African shelled Urocyclidae. It must be remembered, however, that at this time he had not yet turned his attention to the African fauna.

*T. chionobasis* comes close to a number of species of the *T. plicatula* (von Martens, 1869) group. The form of that species described as *Bloyetia erlangeri* Kobelt, 1905 is white not brown above but does have a deep blue apex; *Ledoulxia connollyi* Haas, 1932 is a brown shell with a pale peripheral band and pale apex. One of the paratypes of *Bloyetia kismayuensis* Kobelt, 1905 preserved in the British Museum (Nat. Hist.) has a black apex but pale upper side of the shell whereas another has a brown spire but pale apex but may well be broadly conspecific with *T. chionobasis*. *T. peliostoma* von Martens, 1882 is distinct in its blackish brown aperture interior. Finally the material wrongly referred to *Bloyetia revoili* by Connolly (*Atti Soc. Mat. Nat. Modena* (6) **7** (1928), p. 121) could well be the same as *T. chionobasis*. References to all these species are given by Bacci (1951) and Verdcourt (1960) (see above) and are not repeated here. It is not known how useful the various colour patterns mentioned are for sorting out species; it seems likely they are very variable and of little value. Very few specimens have been dissected. Enough has been said to draw the attention of a future reviser to the nature of Pilsbry's species and to ensure it is not overlooked.

BERNARD VERDCOURT

Spring Cottage, Kimbers Lane, Maidenhead, Berks. SL6 2QP.

(Received, 20th November, 1986)





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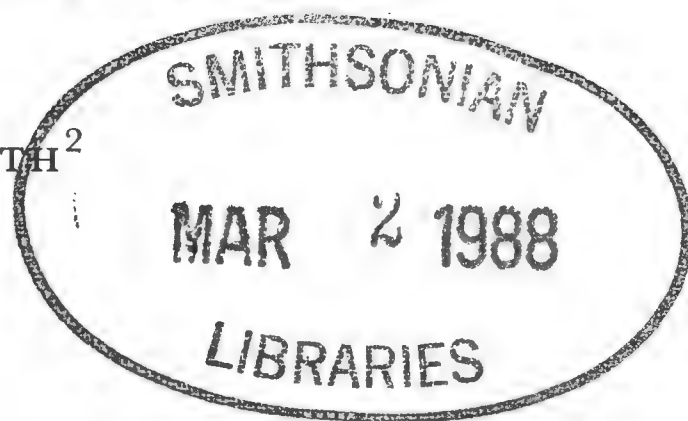
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# LIVING MOLLUSCS OF LAKE TANGANYIKA: A REVISED AND ANNOTATED LIST

D. S. BROWN<sup>1</sup> AND G. MANDAH-BAATH<sup>2</sup>

(Accepted for publication, 15th May, 1987)



**Abstract:** A revised list is presented of recent Bivalvia and aquatic Gastropoda found in Lake Tanganyika and waterbodies in its immediate vicinity. Explanations are given for numerous changes from the nomenclature and systematics in previous monographic treatments of this fauna (Leloup 1950, 1953). The aquatic molluscs found in Kigoma, Ujiji and the northern part of the Malagarasi delta during a short collecting expedition in 1979 are reported. The revised total of 15 bivalve species includes 9 endemic species and one endemic subspecies; *Eupera ferruginea* (Sphaeriidae) is reported for the first time from Lake Tanganyika. The revised total of 60 gastropod species includes 36 endemic species and one endemic subspecies. Seven gastropod taxa in Leloup's list appear to have been recorded in error from Lake Tanganyika: '*Vivipara*' *costulata* Martens, *Lanistes farleri* Craven, '*Melania*' *tanganyicensis* Smith, '*Cleopatra*' *trisulcata* Germain, '*Planorbis*' *apertus* Martens, '*Planorbis*' *lamyi* Germain and *Biomphalaria choanomphala* (Martens). The 13 additional gastropod species recognised arise from the splitting of Leloup's taxa as well as adding species reported by subsequent authors. The presence of the planorbid genera *Afrogyrus*, *Ceratophallus* and *Segmentorbis* was confirmed by dissection of recently collected animals. *Cleopatra trisulcata* Germain is transferred to the genus *Bellamya*. The synonymy is proposed of *Vivipara bridouxiana* Bourguignat, 1888 with *Cleopatra guillemei* Bourguignat, 1885.

## INTRODUCTION

Lake Tanganyika is famous for its endemic prosobranchs; an ancient fauna of obscure origins, diverse in shell form, ornamentation and habitat, and so unlike the usual run of freshwater shells that early students thought immediately of marine shell-forms. The term 'thalassoid' (marine-like) was coined by Bourguignat (1885a) and 'halolimnic' by Moore (1903), but it is now generally accepted that all the endemic molluscs of Lake Tanganyika are descended from freshwater stocks and have evolved their special characters within the lake. Brief histories of knowledge of the lake's molluscs are given by Boss (1978), Brown (1980) and Beadle (1981).

A strictly lacustrine molluscan fauna, of the sub-littoral and open shores exposed to wave-action, is dominated by endemic prosobranchs and bivalves. Distinguishable from this group are the molluscs living in tributaries, lake-side swamps, tenuously connected marshes and pools; some are endemic prosobranchs, but this fauna is dominated by pulmonates and prosobranchs that are widespread in the Tanganyika basin and beyond.

The whole biota of Lake Tanganyika is of great scientific interest, and in recent years concern has been expressed that it could suffer damage, possibly irreversible destruction, from pollution that might ensue if oil is discovered in the lake basin. It appears likely that the interest of the international scientific community in Lake Tanganyika will intensify, in order to gain a better knowledge of its life before serious damage can occur, and to promote biological conservation in the lake basin.

Impressive systematic treatments of the Mollusca of Lake Tanganyika by Leloup (1950, 1953) are remarkable for numerous, fine illustrations of shells. Leloup greatly simplified the

<sup>1</sup> Department of Zoology, British Museum (Natural History), London SW7 5BD, UK. (D. S. Brown is a member of the external Scientific Staff of the Medical Research Council).

<sup>2</sup> Marskvej 11, Vesterlund, Nr Nebel, DK-6830 Denmark.

taxonomy by lumping many species regarded as distinct by previous authors. His classification was reproduced with minor changes by Boss (1978), who considered Lake Tanganyika among other ancient lakes, when comparing pulmonates with prosobranchs in respect of their lacustrine radiations. Unfortunately, Leloup's classifications are seriously out of date, and his account of gastropods is marred by a number of errors, some of which were corrected by Brown (1980a, Table 29, p. 405).

Our present purpose is to list the molluscs living in and around Lake Tanganyika, explaining in some detail the numerous changes from the nomenclature and systematics of Leloup. Sources of reference are provided for the reader requiring further information. For species found outside Lake Tanganyika there is a summary of their total distributions. The opportunity is taken to provide information resulting from a brief collecting expedition to the Kigoma area in 1979.

This list is far from being complete or definitive. Changes from Leloup's account mostly affect taxa that are not strictly lacustrine, and especially the pulmonates, on which research has been concentrated in recent decades. For the endemic prosobranchs, knowledge has advanced hardly at all since Leloup's studies, but it appears likely that a number of the nominal species with varied shell form will be subdivided when observations have been made on features such as chromosome number and enzymes, in conjunction with precise ecological studies. However, we believe that the present list provides a sound basis for advances in molluscan studies in the context of cataloguing and conserving the life of Lake Tanganyika.

#### REVISION OF LELOUP'S LISTS

To the left, bivalves and gastropods are listed in the order used by Leloup (1950, 1953) and with the prosobranchs divided into the same two groups, 'ordinary' and 'thalassoid'. To the right are corresponding names that we believe to be most appropriate. Changes from Leloup's names are explained in notes, indicated here by superscript numbers and listed in the following section; notes for bivalves and gastropods are in separate series. The abbreviation Bgt is used for Bourguignat.

#### Class Bivalvia

##### Family Cyrenidae

*Corbicula fluminalis* (Müller, 1774)

*Corbicula fluminalis tanganyicensis*<sup>1</sup> Crosse, 1881

##### Family Sphaeriidae

*Sphaerium hartmanni* (Jickeli, 1874) var. *congicum* Haas, 1936

*Pisidium giraudi* Bgt, 1885

*Sphaerium bequaerti* (Dautzenberg & Germain, 1914)<sup>2</sup>

*Pisidium giraudi*<sup>3</sup>

*Eupera ferruginea* (Krauss, 1848)<sup>4</sup>

##### Family Unionidae

##### Subfamily Parreysiinae

*Parreysia nyassaensis* (Lea, 1864)

*Caelatura ujijiensis* Crosse, 1881<sup>5</sup>

##### Subfamily Caelaturiinae

*Caelatura (Caelatura) aegyptiaca* (Cailliaud, 1827)

form *horei* Smith, 1880

*Caelatura horei* (Smith)<sup>6</sup>

form *niloticus* (Cailliaud, 1827)

form *calathus* (Bgt, 1885)

*C. (Grandidieria) burtoni* (Woodward, 1859)  
form *typica* and 3 other forms

*Caelatura burtoni*<sup>7</sup>

Subfamily Brazzaeinae

*Brazzaea anceyi* Bgt, 1885

*Brazzaea anceyi*

Family Mutelidae

Sub-family Aspathariinae

*Aspatharia (Spathopsis) kirki* (Ancey, 1894)

*Spathopsis nyassaensis* (Lea, 1864)<sup>8,9</sup>

*A. (Spathopsis) rubens* (Lamarck, 1819)

form *chaiziana* Rang, 1835

*Spathopsis wissmanni* (Martens, 1883)<sup>10</sup>

Subfamily Etheriinae

*Etheria elliptica* Lamarck, 1807

Family Etheriidae

*Etheria elliptica*<sup>11</sup>

Sub-family Mutelinae

*Mutela (Mutela) soleniformis* Bgt, 1885

form *moineti* (Bgt, 1886)

*Mutela soleniformis*<sup>12</sup>

*Moncetia lavigeriana* Bgt, 1886

*Spathopsis anceyi* (Bgt, 1885)<sup>13</sup>

Sub-family Iridininae

*Iridina (Cameronia) spekii* Woodward, 1859

*Mutela spekei*<sup>14</sup>

Sub-family Pseudospathinae

*Pseudospatha tanganyicensis* (Smith, 1880)

form *typica* and 5 others

*Pseudospatha tanganyicensis*<sup>15</sup>

## Class Gastropoda

Subclass Euthyneura: Order Basommatophora

Family Lymnaeidae

*Lymnaea (Radix) natalensis* Krauss, 1848

*Lymnaea (Radix) natalensis*

Family Planorbidae

*Bulinus (Bulinus) angolensis* (Morelet, 1866)

*Bulinus coulboisi* (Bgt)<sup>1,2</sup>

*B. natalensis*<sup>3</sup>

*B. (Physopsis) africana* (Krauss, 1848)

Possibly a mixture of *B. africanus* and *B. globosus* (Morelet); see note 4

*B. (Pyrgophysa) forskalii* (Ehrenberg, 1831)

*B. forskalii*

*B. scalaris* (Dunker)<sup>5</sup>

Subfamily Planorbinae

*Biomphalaria alexandrina*

form *tanganyicensis* (Smith, 1881)

form *pfeifferi* (Krauss, 1848)

form *choanomphala* (Martens, 1879)

Note 6

*Biomphalaria sudanica* (Martens)<sup>7</sup>

*B. pfeifferi*<sup>8</sup>

*B. choanomphala*(?)<sup>9</sup>

*Planorbis (Gyraulus) apertus* Martens, 1897

*Gyraulus costulatus*(?) (Krauss)<sup>10,11</sup>

*P. (Gyraulus) chevalieri* (Germain, 1904)

*Segmentorbis angustus*(?) (Jickeli)<sup>12</sup>

*P. (Gyraulus) coretus* De Blainville, 1826

Probably a mixture of *Afrogyrus coretus* and *Ceratophallus natalensis* (Krauss) see note 13

*P. (Gyraulus) costulatus* Kraus, 1848

*Gyraulus costulatus*<sup>14</sup>

*P. (Gyraulus) lamyi* Germain, 1905

(?) *Ceratophallus* sp.<sup>15</sup>

*Segmentina kanisaensis* Preston, 1914

*Segmentorbis kanisaensis*<sup>16</sup>

*S. planodiscus* Melvill & Ponsonby, 1897

*Segmentorbis angustus*<sup>17</sup>

possibly mixed with

*Lentorbis junodi* (Connolly)<sup>17</sup>

Family Ancyliidae

Subfamily Ferrissiinae

*Burnupia caffra* (Krauss, 1848)

*Burnupia caffra*<sup>18</sup>



*Ferrissia tanganyicensis* (Smith, 1906)

Subclass Streptoneura (Prosobranchia)

'Prosobranches Ordinaires'

Family Ampullariidae

*Lanistes* (*Leroya*) *farleri* Craven, 1880

*L.* (*L.*) *graueri* Thiele, 1911

*Lanistes* (*Meladomus*) *olivaceus* (Sowerby, 1825) and form *jouberti* (Bgt, 1888)

*Pila ovata* (Olivier, 1804)

Family Viviparidae

*Neothauma tanganyicense* Smith, 1880 and form *bicarinatum* (Bgt, 1885)

*Viviparus*(?) *brincatianus* (Bgt, 1888) and form *bridouxianus* Bgt, 1888

*Viviparus costulatus* Martens, 1892

*V. unicolor* (Olivier, 1804)

Family Hydrobiidae

*Bithynia* (*Parabithynia*) *alberti* (Smith, 1888)

*Mysorelloides multisulcata* (Bgt, 1888)

*Tomichia*(?) *guillemei* Leloup, 1953

Family Melaniidae

Subfamily Melaniinae

*Melania*(?) *tanganyicensis* Smith, 1880

*Melanoides admirabilis* (Smith, 1880)

*M. tuberculata* (Müller, 1774)

Subfamily Paludominae

*Cleopatra bulimoides* (Olivier, 1804)

*C. cyclostomoides* (Küster, 1852)

*C. guillemei* Bgt, 1885

*C. jouberti* Bgt, 1888

*C. trisulcata* Germain, 1905 and form *foai* Germain, 1905

Subfamily Potadominae

*Potadomoides pelseneeri* Leloup, 1953

'Prosobranches Thalassoides'

Family Syrholopsidae

*Anceya* (*Anceya*) *giraudi* Bourguignat, 1882

*A.* (*Burtonilla*) *terebriformis* (Smith, 1890)

*Martelia tanganyicensis* Dautzenberg, 1908

*Syrholopsis gracilis* Pilsbry & Bequaert, 1927

*S. lacustris* Smith, 1880

Family Melaniidae

*Bathanalia howesii* Moore, 1898

*B. straeleni* Leloup, 1953

*Bridouxia giraudi* Bgt, 1885,

*Ferrissia tanganyicensis*<sup>19</sup>

*Lanistes farleri*<sup>20</sup>

*L. graueri*<sup>21</sup>

*L. ovum*<sup>22</sup>

*Pila ovata*<sup>23</sup>

*Neothauma tanganyicense*<sup>24</sup>

*Cleopatra guillemei* Bgt<sup>25</sup>

*Bellamya costulata*<sup>26</sup>

*Bellamya capillata*(?)<sup>27</sup>

Note 28

*Gabbiella humerosa tanganyicensis*

Mandahl-Barth<sup>28,29</sup>

*M. multisulcata*<sup>30</sup>

*Tomichia*(?) *guillemei*<sup>31</sup>

Thiaridae<sup>32</sup>

Thiarinae

*Melanoides polymorpha* (Smith)<sup>33</sup>

*Melanoides admirabilis*

*M. tuberculata*<sup>34</sup>

*Cleopatra ferruginea*<sup>35</sup>

*C. ferruginea* (I. & H. C. Lea)<sup>35</sup>

*C. guillemei*<sup>36</sup>

*C. guillemei*(?)<sup>37</sup>

*Bellamya trochlearis*(?) (Martens)<sup>38</sup>

*Potadomoides pelseneeri*<sup>39</sup>

Note 40

*A. giraudi*<sup>41</sup>

*A. terebriformis*<sup>41</sup>

*Martelia tanganyicensis*

*Syrholopsis gracilis*

*S. lacustris*<sup>42</sup>

*S. minuta*<sup>42</sup>

Thiaridae<sup>32</sup>

*Bathanalia howesii*

*B. straeleni*<sup>43</sup>

*Bridouxia giraudi*<sup>44</sup>

*B. praeclara* Bgt)<sup>44</sup>

	<i>B. leucoraphe</i> (Ancey) <sup>44</sup>
	<i>B. smithiana</i> (Bgt) <sup>44</sup>
	<i>B. ponsonbyi</i> (Smith) <sup>44</sup>
	<i>B. rotundata</i> (Smith) <sup>44</sup>
<i>Chytra kirkii</i> (Smith, 1880)	<i>Chytra kirkii</i>
<i>Edgaria nassa</i> (Woodward, 1859)	
form <i>typica</i>	<i>Lavigeria nassa</i> <sup>45,46</sup>
form <i>giraudi</i> (Bgt, 1885)	<i>L. nassa</i>
form <i>globosa</i> (Ancey, 1898)	<i>Hirthia globosa</i> <sup>47</sup>
form <i>grandis</i> (Smith, 1881)	<i>Lavigeria grandis</i>
form <i>paucicostata</i> (Smith, 1881)	<i>L. nassa</i>
form <i>spinulosa</i> (Bgt, 1885)	<i>L. nassa</i>
<i>Hirthia littorina</i> Ancey, 1898	<i>Hirthia littorina</i>
<i>Limnotrochus thomsoni</i> Smith, 1880	<i>Limnotrochus thomsoni</i>
<i>Paramelania</i> ( <i>Bythoceras</i> ) <i>iridescent</i> (Moore, 1898)	<i>Paramelania iridescent</i>
<i>P.</i> ( <i>Paramelania</i> ) <i>damoni</i> (Smith, 1881)	<i>P. damoni</i>
<i>Reymondia horei</i> (Smith, 1880)	<i>Reymondia horei</i> <sup>48</sup>
	<i>R. pyramidalis</i> Bgt, 1888
	<i>R. tanganyicensis</i> Smith, 1889
<i>Spekia zonata</i> (Woodward, 1859)	<i>Spekia zonata</i> <sup>49</sup>
<i>Stanleya neritinoides</i> (Smith, 1880)	<i>Stanleya neritinoides</i>
<i>Stormsia minima</i> (Smith, 1908)	<i>Stormsia minima</i> <sup>50</sup>
<i>Tanganyicia rufofilosa</i> (Smith, 1880)	<i>Tanganyicia rufofilosa</i>
<i>Tiphobia horei</i> Smith, 1880	<i>Tiphobia horei</i>

Notes: *Bivalvia*

1. *Corbicula* forms of great lakes in eastern Africa were classified by Mandahl-Barth (1954a) in *C. africana* (Krauss, 1848), though with the reservation that they might just as well be referred to the racial cycle of *C. fluminalis*, and now we regard *africana* as a subspecies of *fluminalis*. The Lake Tanganyika form of *Corbicula* is related to forms living in the lakes Victoria, Albert and Edward, but since it seems to be smaller and usually more triangular it may be distinguished as the subspecies *tanganyicensis* Crosse.
2. *Sphaerium hartmanni congium* Haas (1936) is, as shown by Mandahl-Barth (1968) a junior synonym of *S. bequaerti* (Dautzenberg & Germain, 1914). Widely distributed in tropical Africa (Mandahl-Barth, Ripert & Raccurt, 1974, as *S. congium*).
3. In the opinion of Leloup, the many shells of *Pisidium giraudi* collected in Lake Tanganyika originated from inflowing streams. However, Kuiper (1961, 1966) believed this species to be truly lacustrine, arguing from the form of the valves and their occurrence in stomachs of fish.
4. *Eupera* is not previously recorded from Lake Tanganyika. *E. ferruginea* (Krauss, 1848) was found in 1979 near Kigoma in a lakeside lagoon and an earth dam (Appendix, 79–9 and 79–14). *E. ferruginea* is a senior synonym of *Eupera* (= *Byssanodonta*) *parasitica* (Deshayes, 1854); it occurs in the lower Nile and much of tropical Africa, and is found in lakes Albert and Victoria (Mandahl-Barth 1954a).
5. The genus *Parreysia* does not include any African species and its distribution is restricted to southern Asia (Haas 1969). Leloup used the name *Parreysia nyassaensis* (Lea) for *Unio nyassaensis* Lea (1864; type-locality, Lake Malawi), treated as a *Caelatura* by Mandahl-Barth (1972). *Unio nyassaensis* variety *tanganyicensis* was described by Smith (1881), but Crosse (1881) changed the varietal name to *ujijiensis* because Smith (1880) had earlier described a '*Unio tanganyicensis*' (here regarded as a form of *Caelatura burtoni*). Leloup

regarded *ujijiensis* and *nyassaensis* as conspecific, but it seems likely that they are distinct species (Mandahl-Barth 1972).

6. *Caelatura horei* is closely related to *C. aegyptiaca*, but probably is a valid species.

7. The genus *Grandidieria* was established by Bourguignat (1885b) for *Caelatura burtoni* (and 24 other species). Haas (1936, 1969) accepted *Grandidieria* as a subgenus of *Caelatura*, but it is superfluous, having no character that cannot be present in other *Caelatura* species, eg, the highly variable *C. hauttecoeurii* (Bourguignat) (see also Mandahl-Barth 1982, pp. 5–6).

8. *Aspatharia* and *Spathopsis* should be treated as distinct genera defined as follows (Mandahl-Barth, 1983):

*Aspatharia* Bourguignat 1885, without a praesiphonal suture and with an umbonal sculpture consisting of parallel, broadly V-shaped ridges.

*Spathopsis* Simpson 1900, with a short praesiphonal suture and an umbonal sculpture consisting of concentric ridges.

9. Although questioned by Mandahl-Barth (1972), Leloup's identification of *Spathopsis kirki* (Ancey, 1894) appears to be correct; this form is not specifically distinct from *Spathopsis nyassaensis* (Lea, 1864, as *Spatha*). This species appears to be restricted to the Shire river, Lake Malawi and Lake Tanganyika. Whether it lives actually in Lake Tanganyika, or rather in tributary rivers is unknown (Leloup 1950).

10. There is a distinctive difference between the hinge plates of *Spathopsis rubens* (Lamarck, 1819) and *S. wissmanni* (Martens, 1883), demonstrated by Pilsbry & Bequaert (1927), but nevertheless subsequent authors (Leloup 1950, Pain & Woodward 1962, Haas 1968) regarded *wissmanni* as a synonym of *rubens*, to which they also referred *Spatha chaiziana* Rang (1835; type locality in Senegal). However, *chaiziana* is an *Aspatharia*, by virtue of the lack of the praesiphonal suture, as described by Rang and confirmed by Daget (1962). The shell illustrated as *S. rubens*, from Nyangwe in eastern Zaire, by Mandahl-Barth (1968, pl. 11, 3) is actually a typical *S. wissmanni*. This species is distributed in West African rivers from Senegal to south east Zaire, and has been found in large rivers near their entry into Lake Tanganyika but not in the lake itself (Leloup 1950).

11. A few shells of *Etheria elliptica* have been reported found on shores of Lake Tanganyika, but Leloup (1950) agreed with Pilsbry & Bequaert (1927) that its occurrence in this lake appeared very doubtful. Nor is *E. elliptica* known from lakes Edward and Albert, but it does live in Lake Victoria (Mandahl-Barth 1954a) and was common during 1971–75 on wave-washed rocks near Kisumu (Brown, original observations).

12. *Mutela soleniformis* appears to be a valid species, comprising thin-shelled and thick-shelled forms (the latter grouped as form *moineti* by Leloup). However, there are similarities to *Mutela dubia nilotica* (Cailliaud), as discussed by Leloup (1950).

13. *Moncetia lavigeriana* Bourguignat (1886) is a junior synonym of *M. anceyi* Bourguignat (1885), which is endemic to Lake Tanganyika (though only empty shells are known). Pilsbry & Bequaert (1927) classified *Moncetia* as a subgenus of *Aspatharia*, but added (p. 413) that 'the subgenus may prove superfluous'. Leloup's drawings of the umbonal sculpture and hinge plate (Fig. 47) agree with *Spathopsis*; it is of course desirable to examine animals to find out if the praesiphonal suture characteristic of this genus is present.

14. The hinge plate in *Mutela* is commonly smooth, but some species develop tubercles to some extent, especially on the posterior hinge plate, and this variation seems to be continuous (see Leloup, Fig. 50). The genus *Iridina* was founded by monotypy on *I. exotica* Lamarck, 1819, which is a form of *Mutela dubia* (Gmelin) with a tuberculate hinge plate (Franc 1949, Lévêque 1974). *Cameronia* Bourguignat, 1879 was named for a specimen of *Iridina spekei* Woodward with particularly strong tubercles. Since *spekei* is closely related to *dubia*, *Cameronia* is a junior synonym of *Iridina* and neither group can be distinguished from *Mutela*.



The strongly tuberculate hinge plate seen in some examples of *Mutela spekei* led many authors including Pain & Woodward (1964) to classify this species in *Pleiodon* Conrad, 1834. However, *Pleiodon* appears to differ from *M. spekei* in having strong tubercles on both the anterior and the posterior parts of the hinge plate. Haas (1969) classified *Pleiodon* as a subgenus of *Iridina* with a single species, known from the recent fauna of Senegal and as a plio-pleistocene fossil from Uganda. To Van Damme (1984, p. 107), *Pleiodon* is of considerable biogeographical interest, as the most widespread and dominant mutelid of the Early and Middle Miocene, and 'now only surviving as a relict in Lake Tanganyika and the Casamance river'. In our view *Pleiodon* possibly is distinguishable from *Mutela* as a subgenus on account of its strongly tuberculate hinge plate, but we are not convinced that possession of such a hinge plate necessarily indicates a close relationship with *Mutela spekei*.

15. Leloup established the subfamily Pseudospathinae for this genus and placed it in the Mutelidae. Pain & Woodward (1968) proved that it actually is a Unionid, but maintained the subfamily, which seems superfluous. Just one variable species, endemic to Lake Tanganyika, is recognisable.

#### Notes: Gastropoda

1. Leloup is among authors who have used subgenera in *Bulinus* incorrectly. Misconceptions and difficulties were discussed by Mandahl-Barth (1958, p. 59) and Brown (1981); if subgeneric names are required, *B. coulboisi* should be classified in subgenus *Isidora*, whereas *B. forskalii* would be properly placed in *Bulinus* s.s.

2. *Bulinus angolensis* is undoubtedly a member of the *B. truncatus/tropicus* complex (Brown 1980a) but its closer relationships are unclear, largely because it has not yet been characterised in terms of its chromosome number, which varies within this complex. Leloup used the name *B. angolensis* for snails from Lake Tanganyika following the opinion of Bequaert & Clench (1931), who considered only shell characters. Leloup united under *B. angolensis* several taxa including *B. coulboisi* (Bourguignat, 1888, 1890; type-locality on the western shore of Lake Tanganyika), which is the senior available name founded on snails belonging to this species-complex and collected in the Tanganyika basin.

The name *B. coulboisi* has been used for snails identified from characters of the shell, radula and copulatory organ, from Lake Tanganyika and smaller lakes and dams in eastern Africa (Mandahl-Barth 1957, 1965; Danish Bilharziasis Laboratory 1978). It cannot be assumed that all these populations are conspecific; probably both diploid and tetraploid populations were included (see note 3).

Observations on morphology, chromosome number and biochemical features of specimens from Kigoma, (Brown, Matovu & Rollinson 1982), led to the conclusion that *B. coulboisi* is tetraploid and conspecific with *B. truncatus* (Audouin, 1827); the latter is common in North Africa and is known from scattered localities in central Africa (Brown & Rollinson 1982).

3. If a diploid member of the *B. truncatus/tropicus* complex occurs in or near Lake Tanganyika, it is likely to be *B. natalensis* rather than *B. tropicus*, which is associated with comparatively cool climatic areas (Brown, Oberholzer & Van Eeden 1971). Both *natalensis* and *tropicus* have been reported to occur near Lake Tanganyika (Danish Bilharziasis Laboratory 1978), though identification was based on morphology without observation of chromosome number.

4. *Bulinus africanus* of Leloup was identified entirely by shell characters, but these by themselves do not adequately differentiate this species from *B. globosus* (Morelet, 1866), which likewise is widespread in eastern Africa. Better, but not entirely satisfactory characters are found in the copulatory organ (Mandahl-Barth 1965, Brown 1966) and certain enzymes (Rollinson & Southgate 1979, Jernes 1979). Both species have been reported to occur on the lake shore (Danish Bilharziasis Laboratory 1978). In 1979, no



snail belonging to the *B. africanus* was found in or near to Lake Tanganyika, but *B. globosus* was obtained near the Malagarasi river at about 100 km north-east from the lake shore (Experimental Taxonomy Unit no. 3482; identification according to the copulatory organ).

The presence of *B. africanus* in the Tanganyika basin requires confirmation; it appears likely that some or even all of Leloup's specimens were *B. globosus*. In Lake Victoria near Kisumu, *B. africanus* was not found on stony beaches or in swamps, where *B. globosus* and *B. ugandae* occurred commonly (Brown 1980a, p. 327).

5. *Bulinus scalaris* (Dunker, 1845) is reported from near both the north and south ends of Lake Tanganyika (Danish Bilharziasis Laboratory 1978). Found usually in temporary rainpools; widely distributed in central and eastern Africa.

6. *Biomphalaria alexandrina* is most recently classified as a monotypic species restricted to Egypt and Sudan (Danish Bilharziasis Laboratory 1978, Brown 1980a); this species-concept excludes all the forms Leloup reported to occur in Lake Tanganyika. Leloup was of the opinion that all his material of *Biomphalaria* belonged to a single species, but it appears that two species may be recognisable; *B. sudanica* and *B. pfeifferi*.

7. Comparatively depressed *Biomphalaria* shells, sometimes with up to 3 angulations, were identified by Leloup as form *tanganyicensis* Smith (1881; as a variety of *Segmentina* (*Planorbula*) *alexandrina*, with type-locality Lake Tanganyika); this taxon was classified by Mandahl-Barth (1958) as a subspecies of *B. sudanica* with the range Central Africa, mainly south of the equator. Typical specimens of *tanganyicensis* are distinctive, with strongly angular whorls, but there is such variation and it does not seem justifiable to separate the extreme form as a distinct subspecies (Brown, 1980a). The range of *B. sudanica* sensu lato extends northwards to Lake Chad, Sudan and Ethiopia.

8. A series of shells with comparatively higher, more rapidly increasing whorls was identified by Leloup as form *pfeifferi*. Such shells, from a large area of central Africa including Lake Tanganyika, were classified by Mandahl-Barth (1958) as *B. pfeifferi* *bridouxiana* (Bourguignat, 1888). However, variation in *B. pfeifferi* does not appear to show a sufficiently clear geographical pattern to justify maintaining subspecies (Brown 1980a). *B. pfeifferi* sensu lato is even more widespread than *B. sudanica*, occurring in much of Africa south of the Sahara.

9. *B. choanomphala* is lacustrine, but it appears doubtful that it occurs in Lake Tanganyika; recently reported distribution is lakes Victoria, Kyoga and Albert, and certain parts of the Nile (Mandahl-Barth 1958, Brown 1980a). A similar form of shell, its whorls high, rapidly increasing and strongly angular, is rare, if present at all, in Lake Tanganyika. Two examples were supposed to have been collected by E. Foà (Germain 1905, 1908); apparently none have been found subsequently, and we think it likely that the shells studied by Germain came from Lake Victoria. High-whorled, angular forms of *Biomphalaria* are found in a number of lakes and appear to be deprived from *B. pfeifferi*; their inter-relationships, and the validity of *B. choanomphala* as a distinct species, need further investigation.

10. Since the time of Leloup's work, the classification of small, discoid planorbids placed in *Planorbis* has been revised, using data from anatomical studies. According to the definitions of genera proposed by Brown & Mandahl-Barth (1973), *Planorbis* lacks a penial stylet and is not found in tropical Africa. *Gyraulus* has a dagger-like penial stylet and is widespread in Africa.

11. *Planorbis apertus* was described by Martens from shells with the locality Lake Edward; its taxonomic position is uncertain because the structure of the copulatory organ is not known for any example from the type-locality. '*Gyraulus apertus* (Martens)' of Starmühlner (1969) was re-named *Afrogyrus starmuehlneri* Brown (1980b); this little planorbid is endemic to highland streams in Madagascar, and it is not closely related to any species known from Africa. Brown (1980a) classified *P. apertus* provisionally in *Ceratophallus* and found that

Leloup's figures of shells represented *Gyraulus costulatus* (Krauss). All 3 specimens of *apertus* reported by Leloup came from Bangwé lagoon, between Kigoma and Ujiji, but the only small planorbids found in 1979 in this lagoon, and in lakeside swamp at Ujiji, were *Segmentorbis angustus* and *Afrogyrus coretus* (see notes 12 and 13 and Appendix: 79–14 and 79–15).

12. Leloup transferred *Segmentina chevalieri* Germain (1904; type-locality Lake Chad) to *Planorbis* (*Gyraulus*), but the comparatively high, lentiform shell clearly conforms to that of African planorbids placed by previous authors in *Segmentina* or *Hippeutis*, both groups founded on Palaearctic species. Anatomical studies of such snails from tropical Africa led Mandahl-Barth (1954a) to segregate them into two new genera, *Segmentorbis* and *Lentorbis*.

The record of *S. chevalieri* Germain from Lake Tanganyika rests on one or more shells from the collection of E. Foà; Germain (1905, 1908) referred to a single shell, Leloup (1953) to two. Treated as a synonym of *S. angusta* (Jickeli, 1874) by Pilsbry & Bequaert (1927), *chevalieri* appears to be described from juveniles of this species (Brown 1980a). However, Leloup found no trace of internal shell septa in Foà's shells from Lake Tanganyika, and this observation raises the possibility that these shells are *Lentorbis junodi* (Connolly). This species has few lamellae or none, and lacks the penial flagellum that is present in *S. angustus*. *L. junodi* is widespread in eastern Africa, but has not so far been identified with certainty from the shore of Lake Tanganyika.

*S. angustus* was obtained in 1979 in the Malagarasi delta and in the lagoon between Kigoma and Ujiji (Appendix, 79–11 and 79–14); 2–5 sets of internal shell lamellae were observed, and dissection showed the presence of the penial flagellum. This snail may be expected to occur in Lake Tanganyika on stony beaches, as it was found beneath wave-washed stones in Lake Victoria, as well as in permanent papyrus swamp (Brown 1980a, p. 327). *S. angusta* is widespread in tropical Africa and is found in Madagascar.

13. Leloup used the name *Planorbis* (*Gyraulus*) *coretus* for small discoid shells, all lacking bodies, 1.1 to 6.5 mm in diameter, and considerably varied in the degree of peripheral angulation. Anatomical studies of snails with the same general shell form led Brown & Mandahl-Barth (1973) to recognise two distinct genera; *Afrogyrus* with the type species *A. coretus* (De Blainville), and *Ceratophallus* with the type species *C. natalensis* (Krauss, 1848). *Afrogyrus* is comparatively small and may be distinguished from the young of *Ceratophallus* by its more slowly increasing whorls, but identifications should be confirmed by examining the penis for diagnostic characters.

*A. coretus*, identified from examination of the penis, was obtained in 1979 in the Malagarasi delta and lakeside marsh at Ujiji (Appendix, 79–11 and 79–14). This snail probably occurs throughout tropical Africa, but it has not previously been identified with certainty from the Tanganyika basin.

Leloup's shells up to about 4 mm diameter may have been *A. coretus*, but bigger specimens, like that shown in his plate 1, fig. 8, may have been *Ceratophallus natalensis*. This snail, identified by examination of the penis, has been found in the northern basin of Lake Tanganyika (Brown & Mandahl-Barth 1973, Fig. 5). *Ceratophallus* sp. here reported from near the Malagarasi delta (Appendix, 79–13) differs in details of penial structure. *C. natalensis* is widespread in eastern Africa, and probably lives in marshes and pools adjacent to Lake Tanganyika, just as it does beside Lake Victoria (Brown 1980a, p. 327).

14. Leloup had only 5 specimens of *Gyraulus costulatus* from Lake Tanganyika, 3 of which he believed to have been washed onto a sandy beach by the river Kalémié. However, it seems likely that there are established populations in Lake Tanganyika, as *G. costulatus* was found, by lifting stones, to be not uncommon on a beach in Lake Victoria (Brown 1980a, p. 326).

15. *Planorbis lamyi* was originally described from two shells in the collection of E. Foà, which according to Leloup were obtained at the southern extremity of Lake Tanganyika.

However, the descriptions by Germain (1905, 1908) do not give any type locality, and it can be only inferred from introductory remarks (Germain 1905) that *P. lamyi* came from Lake Tanganyika or its surrounding region. No more specimens appear to have been found; reasons for rejecting the use of this name for a *Gyraulus* found in South Africa were given by Brown & Van Eeden (1969). Brown (1980a, pp. 164, 405) mentioned that *P. lamyi* might be a lacustrine species of *Ceratophallus*, and excluded it from a list of gastropods of Lake Tanganyika. When examining the type-specimens (Muséum National d'Histoire Naturelle, Paris) in 1980, Brown found resemblances to *C. crassus* (Mandahl-Barth) and *C. kisumiensis* (Preston), both endemic to Lake Victoria. It seems possible that the actual origin of the shells described as *P. lamyi* was not Lake Tanganyika but Lake Victoria (see Discussion).

16. *Segmentina kanisaensis* Preston is the type-species of the subgenus *Segmentorbis* (*Acutorbis*=*Carinorbis*) Mandahl-Barth (1954b, 1956). True *Segmentina* are not found in tropical Africa. The depressed, sharply carinate shell is easily identifiable. Two shells reported on by Leloup, from an affluent river near Albertville, may be the first record for Lake Tanganyika, yet *S. kanisaensis* is widespread in tropical Africa. None were found in 1979, but probably this snail lives in marshes adjacent to Lake Tanganyika as it does beside Lake Victoria (Brown 1980a, p. 327).

17. *Segmentina planodiscus* was transferred to *Segmentorbis* by Mandahl-Barth (1954a). The distinction between this species and *S. angustus* is doubtful; the distribution of *planodiscus* is given as the coastal area of eastern South Africa (Brown 1980a). Of the shells identified by Leloup, those with internal shell lamellae appear to be *S. angustus* (see note 12), and those stated to lack lamellae (Leloup, p. 47) possibly were *Lentorbis junodi* (see note 12).

18. Shells of *Burnupia caffra* were obtained from sand or fine sediment, from the beach down to a depth of 116 m, but the only complete animals were found on the trunk of a *Borassus* palm dredged from between 70 and 100 m depth (Leloup 1953, p. 50). Although *Burnupia* does not live on sand or fine sediment, it probably lives in Lake Tanganyika where there are suitable surfaces for attachment in shallow as well as deep water; in Lake Victoria, *Burnupia* was found commonly on wave-washed stones (Brown 1980a, pp. 326, 408). Possibly the populations of *Burnupia* in these two lakes are conspecific. The reported distribution of *B. caffra* extends from South Africa to Ethiopia (Brown 1980a).

19. *Ferrissia tanganyicensis* possibly is a local endemic, but knowledge of species in this genus is little advanced, and it is quite likely to be not different from one or more nominal species occurring outside the Tanganyika basin. In Lake Tanganyika, living *Ferrissia* appear to have been obtained only in the Malagarasi delta (Leloup, p. 54). It may be expected to occur on stony beaches, as in Lake Victoria *F. kavirondica* lived on wave-washed stones in company with *Burnupia* (Brown 1980a, pp. 149, 326).

20. It is doubtful whether *L. farleri* occurs in the Lake Tanganyika basin or has ever been found there. The only evidence is that Bourguignat (1890) gave the locality 'bords du lac, près l'embouchure du Malagarazi' for *Leroya bourguignati* Grandidier (1887), a synonym of *Lanistes farleri*, which otherwise seems to occur only in the coastal region of Tanzania and on Zanzibar (Brown 1980a). Grandidier (1887, pp. 193–94) states that *Leroya bourguignati* was found in the basins of either the Kyngani or the Vouami river, which enter the Indian Ocean opposite Zanzibar, and he mentioned no other locality. We have not seen *Lanistes farleri* from any part of the Lake Tanganyika basin; it appears that Bourguignat was mistaken in giving this locality for *L. bourguignati*. The operculum of *L. farleri* illustrated by Leloup (Fig. 72 W) is in a reverse position compared with almost all other opercula in the same figure (see note 50).

21. *Lanistes graueri* was included in the fauna of Lake Tanganyika by Leloup with doubt, on account of a locality near Uvira given by Germain (1916). No other finding of this species in the Lake Tanganyika basin has been reported. It is therefore interesting that a



shell similar to Thiele's original figure of *graueri* was collected near Kigoma, on 'prison beach', by Dr. D. Matovu in 1978. This shell (Experimental Taxonomy Unit No. 3503), though damaged, has no trace of an angulation at the shoulder, commonly seen in *L. graueri* from eastern Zaire (Brown 1980a). It is similar to the form of *L. stuhlmanni* Martens known from Ifakara in southern Tanzania (Brown 1980a). Both Thiele (1911) and Germain (1916) regarded *graueri* and *stuhlmanni* as closely related; whichever name is used, at least one species of *Lanistes* (*Leroya*) seems to live on or close to the shore of Lake Tanganyika, most probably in affluent rivers and streams.

22. The name *Lanistes olivaceus* (J. Sowerby, 1825) must be rejected because of *Ampullaria olivacea* Lamarck (1816, *Encycl. Méthod.*, Pl. 457, fig. 1) which is a synonym of *L. varica* (Müller, 1774) of West Africa. Although Lamarck (1822, *Hist. Nat. Anim. sans Vertèbres*, 6, 2, p. 178) altered the name to *A. guineaica*, that name had already been used by Chemnitz (1786, *Systematisches Conchylien Cabinet*, 9, p. 80) for the same shell as Müller's *varica*.

*L. ovum* from the shores of Lake Tanganyika varies in shape, from the globose shell named *Meladomus jouberti* Bourguignat (1888) to a high-spired form corresponding to *Lanistes olivaceus* form *procerus* Martens (1866). Commenting on such variation, Mandahl-Barth (1968) wrote 'the supposed subspecies almost certainly are nothing but ecological forms, as they are not confined to particular geographical areas'. *L. ovum* appears to be confined to marginal swamps, tributary streams and rivers of Lake Tanganyika (Leloup); its distribution extends over much of tropical Africa.

23. Pain (1961, pp. 11–12) classified all forms of *Pila* from the shores of Lake Tanganyika as *P. ovata ovata*, including 2 shells from Kigoma figured by Leloup (Pl. 3G) with the name *P. wernei*. According to Pain (1961, p. 12) typical *P. wernei* (Philippi) is unknown from the vicinity of Lake Tanganyika, but he included, apparently by mistake, a record of this species from the Malagarasi swamp (repeated by Brown 1980). We have not seen any authentic example of *P. wernei* from Lake Tanganyika. *Pila* like *Lanistes* lives in swamps and tributaries but apparently not on the open shore of Lake Tanganyika (Leloup, p. 68). However, it may possibly be found in the main lake, as *P. ovata* occurs in Lake Victoria on stony beaches (Brown 1980, p. 326) and has been found in deeper water down to 30 feet (Mandahl-Barth 1954, p. 43). *P. ovata* was found uncommonly compared with *Lanistes ovum* in 1979 between Kigoma and Ilagala.

24. The causal connection, suggested by Leloup (p. 83) between a soft substratum and the development of carinations in the shell has yet to be proved. The report of *Neothauma* occurring in Lake Malawi (Crowley, Pain & Woodward 1964) is incorrect; the species in question, *N. ecclesi* Crowley & Pain, was transferred to *Bellamyia* by Mandahl-Barth (1972).

25. Both *Vivipara brincatiana* and *Vivipara bridouxiana* were described by Bourguignat (1888, 1890) and given the same type-locality; the eastern shore of Lake Tanganyika near the mouth of the Malagarasi river. Bourguignat's figures of these shells and *Cleopatra guillemei*, also from near the mouth of the Malagarasi river, represent, in our opinion, a single species of *Cleopatra*. For this the correct name is *C. guillemei* Bourguignat (1885), which is the earliest and therefore the valid spelling. The shells described by Bourguignat have variably developed basal ridges, as does *C. guillemei* from near Lake Victoria, though the ridges may be obsolete in large shells (these were erroneously described as the distinct species *C. nyanzae* Mandahl-Barth, 1954).

*Vivipara brincatiana* has already been treated as a synonym of *Cleopatra guillemei* by Brown (1980a, p. 110). We now propose the new synonymy: *Vivipara bridouxiana* Bourguignat, 1888 = *Cleopatra guillemei* Bourguignat, 1885.

For *Cleopatra jouberti* Bourguignat (1888) the type-locality was also given as the shore of Lake Tanganyika near the mouth of the Malagarasi river. Of two types (Muséum National d'Histoire Naturelle, Paris) from Bourguignat's collection, one shell has a single basal ridge (Pl. 28A) and the other has 3 basal ridges (Pl. 28B). The presence of one or more basal



ridges suggests that *C. jouberti*, although it has a comparatively broad ultimate whorl, is a form of *C. guillemei*.

*C. guillemei* is distinguishable by the presence of basal ridges from the only other *Cleopatra* found near Lake Tanganyika, *C. ferruginea* (see Note 35). A few other specimens were referred directly to *C. guillemei* by Leloup (see Note 35). This snail is reported to occur also at Singida in central Tanzania, and lives in rainpools near the eastern shore of Lake Victoria (Brown 1980a, p. 327).

26. All snails belonging to the Viviparidae and found in Africa, apart from *Neothauma* (endemic to Lake Tanganyika), are classified by recent authors in *Bellamya*.

Leloup's report of *Vivipara costulata* Martens from Lake Tanganyika rests on the use of this name by Germain (1908) for specimens in the collection of E. Foà, from 'the southern part of the lake'. A similar shell, also supposedly from Lake Tanganyika, was named *Vivipara foai* by Germain (1905). Both forms were figured by Leloup (Pl. 3, 4b and 5), and they resemble *Bellamya costulata* (Martens), but this is now regarded as an endemic species of Lake Victoria (Danish Bilharziasis Laboratory 1973, Brown 1980a). The only specimens of *Bellamya* obtained in or near to Lake Tanganyika since the time of Foà are, it appears, a series from the Pala area, identified by Leloup as *Vivipara unicolor* (see below). We therefore think it unlikely that *B. costulata* lives in Lake Tanganyika; more probably the specimens first reported on by Germain came from Lake Victoria (see Discussion).

27. The specimens of *Vivipara unicolor* from Pala identified by Leloup could be *Bellamya unicolor* or *B. capillata* (Frauenfeld). The Tanganyika basin is in an area of apparent overlap between the southern range of *unicolor* and the northern range of *capillata*, and possibly the two taxa are conspecific (Brown 1980a). Their combined distribution extends over most of tropical Africa, but occurrence is scattered, and *Bellamya* is remarkably uncommon in the vicinity of Lake Tanganyika.

28. The family Bithyniidae can be separated as a group distinct from the Hydrobiidae sensu lato of Leloup and earlier authors (see Davis 1979, p. 7). Many African species once placed in *Bithynia* have been removed from the genus (Mandahl-Barth 1968); *Bithynia* sensu stricto occurs in Europe, Asia and north west Africa, but not in the Afro-tropical region. The subgenus *Parabithynia* is founded on a species living in India that is not closely related to any bithyniid found in Africa (Mandahl-Barth 1968). The most widespread bithyniid group in Africa is the genus *Gabbiella* Mandahl-Barth (1968), which includes the one bithyniid species found in the vicinity of Lake Tanganyika.

29. In the classification of Mandahl-Barth (1968), *Bithynia alberti* Smith (1888) is *Gabbiella humerosa alberti*, endemic to Lake Albert, while *Bithynia alberti* of Leloup is *G. humerosa tanganyicensis*, found in marshes and tributaries of Lake Tanganyika, but apparently not living in the open lake (Leloup). Leloup (Fig. 72 M) shows the spiral in the operculum nucleus incorrectly as dextral (turning clockwise from the origin) instead of sinistral. In 1979, *G. h. tanganyicense* was found in a small pool beside the Malagarasi river (Appendix, 79–12); none were found in any locality nearer to the lake. The scarcity of *Gabbiella* in Lake Tanganyika is remarkable, in view of the abundance of *G. humerosa* on fine sediment in Lake Victoria (Brown 1980a, p. 326).

30. *Mysorelloides multisulcata* has a cuticular operculum and basal denticles are lacking from the central tooth in the radula (Leloup): this monotypic genus seems better classified in the Thiaridae (Brown, 1980a) than in the Hydrobiidae or the Bithyniidae.

31. Leloup gave the name (?) *Tomichia guillemei* to shells which he believed to have been carried into the lake by a river. Since both the operculum and body are unknown, the taxonomic position of this snail is highly uncertain. It is one of 3 species provisionally classified in *Tomichia* and known from central Africa, which are in need of thorough anatomical study to determine their relationships to the species of *Tomichia* known from South Africa and classified in the family Pomatiopsidae by Davis (1979, 1981).

32. Thiariidae is generally used in preference to Melaniidae in modern classifications of the Gastropoda, following Taylor & Sohl (1962). Definitions of subfamilies, and even of the family, are debatable (Brown 1980a, pp. 83–84) and a comprehensive revision is needed (see also Discussion).

33. The shell named *Melania tanganyicensis* by Smith (1880) looks very much like some forms of *Melanoides polymorpha* (Smith, 1877), which is a species endemic to Lake Malawi: since such a snail has not been refound in Lake Tanganyika, it is more likely that it was collected in Lake Malawi than in Lake Tanganyika (Mandahl-Barth 1972, Brown 1980a).

34. The shell figured as *Melanoides tuberculata* by Leloup (Pl. 2, 4) is not this species but a slender form of *Paramelania* (eg, Leloup, Pl. 11, 2D extreme right). *M. tuberculata* is widespread in Africa and Asia; although found in tributaries of Lake Tanganyika it is apparently absent from the main body of the lake (Leloup), which is surprising in view of its great abundance on fine sediments in other lakes (Mandahl-Barth 1954a, Brown 1980a).

35. *Cleopatra* has been found infrequently in or near to Lake Tanganyika, and most of the specimens come from the Malagarasi delta. Some of the Malagarasi specimens are *C. guillemei* (note 25); the other shells reported by Leloup are considered here together with specimens collected in 1979 (Appendix, 79–11 and 79–12). Leloup separated three shells from the same creek (locality no. 145) into *C. bulimoides*, for the 2 smaller shells (4–5 mm long), and *C. cyclostomoides* for the single larger shell (10 mm long), because he found resemblances to examples of these species from the Nile valley. However, the name *C. bulimoides* (with *cyclostomoides* as synonym) is employed by recent authors for a species that is widespread in northern Africa but reaches its southern limit in northern Kenya (Brown 1980a); its umbilicus is generally open and the lower whorls may be smooth or carinate. The most widespread *Cleopatra* reported for Tanzania, and from central Africa as a whole, is *C. ferruginea*, in which the lower whorls altogether lack carination and the umbilicus is usually closed. Leloup's *bulimoides* and *cyclostomoides* are apparently conspecific; the former has an angular base to the aperture as is usual in young *Cleopatra*. This form is represented by seventeen additional specimens collected in the Malagarasi delta in 1979 (Appendix 79–11 and 79–12); they have a narrow umbilical opening and the largest shell is apparently nearly fully grown at 12 mm length. We identify this form as *C. ferruginea* while pointing out it is unusual for this species to be so widely perforate and so small (full grown *C. ferruginea* usually exceed 20 mm in length).

A single shell from Lake Tanganyika at Sumbu (Danish Bilharziasis Laboratory, leg. McCullough, 1957) has a peripheral carination; with an estimated shell length of 16 mm, this shell is hardly juvenile and we cannot readily assign it to any known form; possibly it represents an undescribed lacustrine species.

We would add that the shells discussed here entirely lack basal ridges, which usually are present in *C. guillemei*.

36. The specimens of *Cleopatra guillemei* reported as such by Leloup (p. 99) were collected at Pala by R. P. (= Révérend Père) Guillemé of the Order of White Fathers (Leloup, p. 93). Guillemé may not be the same man as the R. P. Guillemet, to whom *C. guillemei* was intended to be dedicated (Bourguignat 1890, p. 46, explained in a footnote that the 't' was left out by the printer of the original description). Leloup fails to show the spiral nucleus in opercula (Fig. 72 I and BB) of *C. guillemei* and *C. bulimoides*. Leloup referred also to *C. guillemei* a single shell from the collection of E. Foà (Germain 1908); see note 25 for additional taxa referable to this species, and its distribution.

37. *Cleopatra jouberti* Bourguignat (1888) is possibly a form of *C. guillemei* Bourguignat (1885) (see Note 25).

38. Germain (1908) discussed a resemblance between his *Cleopatra trisulcata* founded on shells believed to have been collected in Lake Tanganyika by E. Foà and *Vivipara cochlearis* Martens (typographical error for *trochlearis*), which is now classified as a species of *Bellamya*

endemic to Lake Victoria (Brown 1980a). Germain's reasons for placing *trisulcata* in *Cleopatra* are unconvincing; shells figured by Germain (1908) and Leloup undoubtedly are a *Bellamya*, as are the type-specimens (Muséum Nationale d'Histoire Naturelle, Paris) (Pl. 28, C and D). As the resemblance to *B. trochlearis* is strong (compare with Brown 1980a, Fig. 20 b), and no such snails have been re-found in Lake Tanganyika, it seems likely that the shells named by Germain were obtained in Lake Victoria, and in fact they may be *B. trochlearis*.

39. The name *Potadomoides* was made up by Leloup in the belief that *P. pelseneeri* was closely related to *Potadoma*. *Potadomoides* lacks, however, the long radula with its quadrangular ridged central tooth which is present in *Potadoma* and other members of the subfamily Melanatriinae. *P. pelseneeri* has been found only in the Malagarasi delta; other members of this genus, with strongly ornamented shells, live in the rivers Luvua and Lualaba to the west of Lake Tanganyika. Brown (1980a) placed *Potadomoides* in the Paludominae and suggested that the genus might represent the ancestral stock from which 'thalassoid' thiarids evolved in Lake Tanganyika. The specimens of *Potadoma ignobilis* reported on by Leloup were collected near Lake Kivu, and this genus has not been found in any locality nearer to Lake Tanganyika.

40. Anatomical studies of *Syrnolopsis* and *Anceya* led to the conclusion that they should be classified in the family Thiaridae (Mandahl-Barth 1954b).

41. It does not seem justifiable to separate the two species of *Anceya* into different subgenera.

42. The operculum of *Syrnolopsis* is paucispiral (Mandahl-Barth 1954b), not concentric as it is illustrated by Leloup (Fig. 72 L). Brown (1980a) accepted as *Syrnolopsis lacustris* only the large, smooth shells among a large number of examples of this species figured by Leloup (Figs. 68, A–D); smaller and carinate shells figured by Leloup (Figs. 68 E–F) were segregated by Brown as *S. minuta* Bourguignat. Further data are needed to establish whether or not *S. lacustris* sensu lato is an aggregate of species; it was perhaps unwise of Fryer, Greenwood & Peake (1985) to reproduce the entire figure 68 of Leloup as an example of variation among shells of a single species.

43. The operculum of *Bathanalia straeleni* is described as paucispiral (Leloup, p. 135), but is shown as multispiral, with at least 8 turns (Leloup, Fig. 72 DD).

44. *Bridouxia* Bourguignat (including *Giraudia*, *Baizea*, *Coulboisia* and *Lechaptoisia*) seems to comprise at least 6 apparently valid species. However, any arrangement must be considered provisional, as some taxa are known only as shells and it is the absence of a median cusp on the central tooth that provides the only evident distinction between this genus and *Reymondia* (note 47). Leloup recognised a single highly varied species of *Bridouxia*; Brown (1980a) separated *B. giraudi* Bourguignat, 1885, comprising smooth-shelled forms, from *B. ponsonbyi* (Smith, 1889), with strong spiral sculpture. We think it justifiable to recognise these and 4 additional species:

*B. giraudi*, reaching  $11 \times 7$  mm, with about 5 whorls, of which the ultimate is large.

*B. praeclara* (Bourguignat, 1885) is only half this size, but has one whorl more and a relatively higher spire; it perhaps is represented by Brown (1980a, Fig. 66g). It is the type of *Giraudia*.

*B. leucoraphe* (Ancey, 1890; as *Ponsonbya leucoraphe*),  $5.5 \times 4.2$  mm, with a large last whorl and a well defined umbilical groove (Brown 1980a, Fig. 66f). This seems to be the same as *Baizea giraudi* Bourguignat, 1885, which is a junior homonym of *Bridouxia giraudi* Bourguignat, 1885.

*B. smithiana* (Bourguignat, 1888),  $5 \times 2.5$  mm, with fine spiral striae on a polished surface. This seems to be the same as *Coulboisia giraudi* Bourguignat, 1888, which is another junior homonym of *Bridouxia giraudi* Bourguignat, 1885. Leloup's Fig. 79 does not appear to be this species but *B. ponsonbyi*.



*B. ponsonbyi* (Smith, 1889),  $6.6 \times 4.3$  mm (Brown 1980a, Fig. 66h; measurements given in the text are incorrect), with strong spiral and transverse sculpture. Ancey (1894) created the genus *Lechaptosia* for it.

*B. rotundata* (Smith, 1904; for *Stanleya neritoides* Bourguignat, 1885, 1888, 1890),  $6-7 \times 5$  mm, the most depressed and nearly globose species. The operculum and radula are unknown; doubtfully placing it in *Bridouxia*, we follow Pilsbry & Bequaert (1927).

There is considerable confusion over the structure of the operculum in *Bridouxia*. Smith (1906) described for *Giraudia praeclara* an operculum consisting of a single whorl, but illustrated one with 3 whorls. Leloup illustrated 4 opercula for *Bridouxia giraudi*, all different from Smith's account, either in being entirely multispiral (Fig. 72 J) or having an outer concentric zone (J1, J2, J3). However, Leloup's figures J and J1 are incorrect in showing the spiral as dextral instead of sinistral. The multispiral structure, with 8 close-set turns, in Leloup's fig 72 J is probably wrong because such an operculum is unknown for any other thiarid snail.

45. The textual description of *Lavigeria* Bourguignat (1890, p. 178) has page priority over *Edgaria* Bourguignat (1890, p. 192). *Lavigeria* also has priority, narrowly, on the first appearance of these names (Bourguignat 1888: *Lavigeria coronata*, Pl. 13, figs. 13-14; *Edgaria paucicostata*, Pl. 14, figs. 8-9).

46. The 6 forms of *Lavigeria nassa* recognised by Leloup were revised by Brown (1980a) as follows; form *grandis* was segregated as a distinct species of *Lavigeria*, form *globosa* was transferred to the genus *Hirthisia* (see not 46), and the remaining 4 forms were retained, undifferentiated, under *L. nassa*. It seems likely, from the great diversity of shell forms currently included under *L. nassa*, that this taxon may prove to be an aggregate of distinct species (see Addendum, after Appendix).

The use by Fryer *et al.* (1985) of *L. nassa*, *sensu* Leloup, to illustrate shell variation within a single species was unfortunate; their figures (after Leloup) represent, in our opinion, two genera and at least 3 species (*Lavigeria nassa*, *L. grandis* and *Hirthisia globosa*).

In agreement with Smith (1906), the operculum of *Lavigeria* is described by Leloup (p. 164) as subspiral, with reference to all of his 4 illustrations (Fig. 72 B, G, N and R); it therefore appears that the clearly spiral nucleus shown in Leloup's figs R and N was drawn in error, and in any case the spiral is shown incorrectly as dextral instead of sinistral.

47. *Hirthisia globosa* Ancey (1898) does not appear to be merely a depressed form of *L. nassa* as supposed by Leloup. From its shell shape and sculpture it appears to have been classified correctly by Ancey (1898) as a congener of *Hirthisia littorina*.

48. It seems impossible to make any clear distinction between shells of *Reymondia* and *Bridouxia*. Possibly *Reymondia* is separable by the presence on the central radular tooth of a median cusp (absent from some at least of *Bridouxia* species), but the radula is known apparently only for typical *R. horei* (Smith 1880, Leloup Fig. 57 DD). A single species was recognised by Leloup (1953) and Brown (1980a), but this has so variable a relationship between shell size and whorl number that at least 3 species may be valid:

*R. horei*,  $16 \times 9$  mm, with about 6 whorls (Brown 1980a, Fig. 66c).

*R. pyramidalis* Bourguignat, 1888,  $7-9 \times 3-4$  mm, with 8 whorls. Probably this is the same as *R. minor* Smith, 1889 (Brown 1980a, Fig. 66d).

*R. tanganyicensis* Smith, 1889;  $3.5 \times 1.7$  mm, with 5 whorls (Brown 1980a, Fig. 66e).

It may be noted, to avoid possible confusion, that although Leloup's Fig. 105 is titled '*Reymondia horei*', the majority of shells illustrated (C-U) are of forms he treated under *Bridouxia*.

49. The operculum of *Spekia* is illustrated inaccurately by Leloup (Fig. 72 O) as being entirely concentric; it has in fact an obvious spiral nucleus with about 2 turns.

50. The operculum of *Stormsia* illustrated by Leloup (Fig. 72, U, not V as given in his



text) is seen from the inner side and with the basal margin towards the top of the page; this position is the reverse of that of other opercula in the same figure apart from W, which is *Lanistes farleri*.

# REVISED LIST OF AQUATIC MOLLUSCS OF LAKE TANGANYIKA AND ITS IMMEDIATE VICINITY

The Unionidae and Mutelidae are listed in the order of Mandahl-Barth (1982, 1983). The Gastropoda follow the order of Brown (1980a).

## Class Bivalvia

### Unionidae

- Caelatura horei* (Smith, 1880)
- C. burtoni* (Woodward, 1859)
- C. ujijiensis* (Crosse, 1881)
- Brazzaea anceyi* Bgt, 1885
- Pseudospatha tanganyicensis* (Smith, 1880)

### Mutelidae

- Spathopsis wissmanni* (Martens, 1883)
- S. nyassaensis* (Lea, 1864)
- S. anceyi* (Bgt, 1885)
- Mutela soleniformis* Bgt, 1885
- M. spekei* (Woodward, 1859)

### Etheriidae

- Etheria elliptica* Lamarck, 1807

### Cyrenidae

- Corbicula fluminalis tanganyicensis* (Crosse, 1881)

### Sphaeriidae

- Sphaerium bequaerti* (Dautzenberg & Germain, 1914)
- Pisidium giraudi* Bgt, 1885
- Eupera ferruginea* (Krauss, 1848)

The Unionidae, *Spathopsis anceyi*, the two *Mutela*, and the *Pisidium* are endemic species, and the *Corbicula* is an endemic subspecies.

## Class Gastropoda

### Subclass Streptoneura (Prosobranchia)

#### Viviparidae

- Bellamya capillata* (Frauenfeld, 1865)
- Neothauma tanganyicense* Smith, 1880

#### Ampullariidae (Pilidae)

- Pila ovata* (Olivier, 1804)
- Lanistes ovum* Peters, 1845
- L. graueri* Thiele, 1911

#### Pomatiopsidae(?)

- Tomichia(?) guillemei* Leloup, 1953

#### Bithyniidae

- Gabbiella humerosa tanganyicensis* Mandahl-Barth, 1968

Thiaridae

Subfamily Thiarinae

*Melanoides admirabilis* Smith, 1880

*M. tuberculata* (Müller, 1774)

Subfamily Syrnolopsinae

*Syrnolopsis lacustris* Smith, 1880

*S. minuta* Bgt, 1885

*S. gracilis* Pilsbry & Bequaert, 1927

*Anceya giraudi* Bgt, 1885

*A. terebriformis* (Smith, 1890)

*Martelia tanganyicensis* Dautzenberg, 1908

Subfamily Paludominae

*Cleopatra ferruginea* (I & H. C. Lea, 1850)

*C. guillemei* Bgt, 1885

*Potadomoides pelseneeri* Leloup, 1953

*Lavigeria nassa* (Woodward, 1859)

*L. grandis* (Smith, 1881)

Subfamily Paramelaniinae

*Mysorelloides multisulcata* (Bgt, 1888)

*Hirthis littorina* Ancey, 1898

*H. globosa* Ancey, 1898

*Spekia zonata* (Woodward, 1859)

*Tanganyicia rufofilosa* (Smith, 1880)

*Stanleya neritinoidea* (Smith, 1880)

*Bridouxia giraudi* Bgt, 1885

*B. praeclara* (Bgt, 1885)

*B. leucoraphe* (Ancey, 1890)

*B. smithiana* (Bgt, 1888)

*B. ponsonbyi* (Smith, 1889)

*B. rotundata* (Smith, 1904)

*Reymondia horei* (Smith, 1880)

*R. pyramidalis* Bgt, 1888

*R. tanganyicensis* Smith, 1889

*Stormsia minima* (Smith, 1908)

*Paramelania damoni* (Smith, 1881)

*P. iridescens* (Moore, 1898)

*Bathanalia howesii* Moore, 1898

*B. straeleni* Leloup, 1953

*Tiphobia horei* Smith, 1880

*Limnotrochus thomsoni* Smith, 1880

*Chytra kirki* (Smith, 1880)

Subclass Euthyneura: Order Basommatophora

Lymnaeidae

*Lymnaea (Radix) natalensis* Krauss, 1848

Ancylidae

*Burnupia caffra* (Krauss, 1848)

*Ferrissia tanganyicensis* (Smith, 1906)

Planorbidae

Subfamily Planorbinae

*Afrogyrus coretus* (De Blainville, 1826)

*Ceratophallus natalensis* (Krauss, 1848)

*Gyraulus costulatus* (Krauss, 1848)  
*Lentorbis(?) junodi* (Connolly, 1922)  
*Segmentorbis angustus* (Jickeli, 1874)  
*S. kanisaensis* (Preston, 1914)  
*Biomphalaria pfeifferi* (Krauss, 1848)  
*B. sudanica* (Martens, 1870)

#### Subfamily Bulininae

*Bulinus africanus(?)* (Krauss, 1848)  
*B. globosus* (Morelet, 1866)  
*B. truncatus* (Audouin, 1827) = *B. coulboisi* (Bgt, 1888, 1890)  
*B. natalensis(?)* (Küster, 1841)  
*B. forskalii* (Ehrenberg, 1831)  
*B. scalaris* (Dunker, 1845)

The *Neothauma*, the *Tomichia(?)*, *Melanoides admirabilis*, the Syrnolopsinae, *Potadomoides pelseneeri*, both *Lavigeria*, the Paramelaniinae and the *Ferrissia* make a total of 36 endemic species, and the *Gabbiella* is an endemic subspecies.

### SUMMARY AND DISCUSSION

#### *Bivalves*

Leloup (1950) lists a total of 14 species found in Lake Tanganyika and its tributary rivers. For 3 species Leloup recognised more than one name form, but none of these are maintained here. Seven of Leloup's species appear in our revised list with their names unchanged in both genus and species (though subgenera are not maintained here). Changes from Leloup's classification above the genus-level are the elimination of subfamilies and the removal of *Pseudospatha* from the Mutelidae to the Unionidae.

Changes in genus and/or species-name affect 7 species in Leloup's list and result in the recognition of 2 additional endemic species: *Caelatura ujijiensis* (Cross) for *Parreysia nyassaensis* of Leloup (which we regard as restricted to Lake Malawi and the Shire river), and *Caelatura horei* (Smith) (which we distinguish specifically from *C. aegyptiaca* of North Africa). We give the first record for Lake Tanganyika of the sphaeriid *Eupera ferruginea*. The resulting total of 15 species includes 10 endemic forms; 9 species and 1 subspecies.

Our concept of *Mutela spekei* (placed in *Iridina* (*Cameronia*) by Leloup, and in *Pleiodon* (*Cameronia*) by Pain & Woodward, 1964) reflects the view, in which we follow Martens (1897), that *Iridina* and *Cameronia* are synonyms of *Mutela*. It follows that the tuberculate hinge plate in *M. spekei* does not necessarily indicate a close relationship with *Pleiodon* as known from West Africa. We therefore treat with caution the opinion (Van Damme 1984) that '*Pleiodon*' *spekei* and *Pleiodon* of West Africa are relicts of a single and once widespread branch of mutelid evolution.

#### *Gastropods*

Leloup (1953) lists a total of 54 species and 12 infra-specific named forms found in Lake Tanganyika (excluding *Potadoma*, of which he examined specimens from tributaries of Lake Kivu). Twenty-eight of these species are maintained in our revised list unchanged in genus, species – name and content (though subgenera may not be maintained here); many of these are endemic Thiaridae, for which little if any new information has appeared since Leloup's account. The only change at the family level is that all species placed by Leloup in the Hydrobiidae are transferred here to other families (Hydrobiidae as re-defined by Davis (1979) are unknown from central Africa).

Changes in name and/or content affect 25 of the full species recognised by Leloup and may result from synonymy, nomenclatural change in accordance with current classification, alteration of identifications and sometimes sub-division of Leloup's taxa. Seven taxa in Leloup's list are omitted from our list because we believe them to have been recorded in error from Lake Tanganyika. First, *Planorbis apertus* of Leloup does not appear to be the species described by Martens (1897). The report of *Lanistes farleri* by Bourguignat (1890) appears to lack foundation. '*Melania*' *tanganyicensis* was collected by Joseph Thomson in the course of a journey to Lake Malawi as well as Lake Tanganyika, so there is good reason to think that this shell, never found subsequently in Lake Tanganyika, came from Lake Malawi. It is less easy to account for the 4 species attributed to the collection of Edouard Foà and which we think came from Lake Victoria: *Biomphalaria choanomphala* (note 9), '*Planorbis*' *lamyi* (note 15), '*Vivipara*' *costulata* (note 26) and '*Cleopatra*' *trisulcata* (note 38). Foà did not visit Lake Victoria, and the most northerly place he reached in the great lakes area was the mouth of the Ruzizi river in Lake Tanganyika (Maunoir 1908, carte 1, p. 732).

Our revised list of gastropods found in or close to Lake Tanganyika contains 60 species (of which 36 are endemic species and one is an endemic subspecies). The reduction of Leloup's list has been more than made up by the addition of 13 species: *Bulinus globosus*, *B. scalaris*, *Ceratophallus natalensis* and *Syrnolopsis minuta*, 5 species of *Bridouxia* and 2 species of *Reymondia*, with provisional identifications of *Bulinus natalensis* and *Lentorbis junodi*.

Specimens collected in the Kigoma area in 1979 enabled us to identify *Segmentorbis angustus* and *Afrogyrus coretus* by anatomical as well as shell characters. We also report the finding at Kigoma of a shell of *Lanistes graueri*, of which there is only one previous record for Lake Tanganyika.

The taxonomy of the Thiaridae stands in need of a comprehensive revision of the entire family on a worldwide basis. At all taxonomic levels, definitions will become firm and relationships clear only when more extensive observations become available for a variety of organ systems, supplemented by cytological and biochemical data. The arrangement in our revised list follows that of Brown (1980a), which is a provisional working arrangement. The Syrnolopsinae appears to be a natural group characterised by the slender shell with a columellar fold. *Potadomoides* and *Lavigeria* were placed in the Paludominae because of similarities between the shells of *Cleopatra* and certain *Potadomoides* spp., and between the radulae of the latter and *Lavigeria*. However, the operculum is different in each genus and the last two perhaps could be placed just as well in the Paramelaniinae. Although it seems justifiable to segregate *Cleopatra* into the Paludominae on account of resemblances in the shell, operculum, radula and nervous system to *Paludomus* (*Paludomus*) of Asia (Starmühlner 1974, pp. 135–6), the Paludominae are not distinguishable satisfactorily from the Paramelaniinae. This putative subfamily provides convenient accommodation for diverse genera, with uncertain affinities and likely to be subdivided when better known; our Paramelaniinae corresponds to the group which Leloup (1953) called thalassoid with the addition of *Mysorelloides*.

For the purpose of making comparisons among the thiarid genera living in the Tanganyika basin, the most extensive data available, after the shell, is for the radula, operculum and reproductive system. For the radula, a distinction has been drawn (Pilsbry & Bequaert 1927, Leloup 1953, pp. 233–34) between genera with short lateral and marginal teeth, having stout cusps, and other genera in which the same teeth are long with fine cusps; such differences seem less likely to reflect phylogeny than adaptations to different food resources and substrata. Information for the operculum and reproduction (Pilsbry & Bequaert 1927 and cited authors; Leloup 1953, Mandahl-Barth 1954b, Bouillon 1955) may be summarised by grouping genera as follows (relevant data are entirely lacking for *Hirthisia*).



Operculum entirely paucispiral or subspiral (in *Lavigeria*)

Possibly oviparous: *Syrnolopsis*, *Anceya*, *Chytra*, *Limnotrochus*, *Martelia*

Viviparous: *Bathanalia*, *Potadomoides*, *Lavigeria*

(Reproduction unknown: *Mysorelloides*, *Stanleya*)

Operculum concentric with spiral nucleus

Possibly oviparous: *Cleopatra*, *Paramelania*, *Spekia*

Viviparous: *Reymondia*, *Tiphobia*, *Tanganyicia*

(Reproduction unknown: *Bridouxia*, *Stormsia*)

One must be cautious in looking at these groups for evidence of phylogeny. More knowledge is needed of the structure and ontogeny of the operculum, and apparent cases of oviparity need to be confirmed by direct observation, for in no case have eggs been described; the brood pouch of a viviparous female might be difficult to detect outside of a brief breeding season. Viviparity has involved at least two different modes of adaptation, for *Tanganyicia* broods the young in a pouch opening onto the side of the head, rather than in the lower part of the oviduct as in other genera.

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## APPENDIX

Collections made in 1979 in Kigoma, Ujiji and the northern part of the Malagarasi delta: specimens are stored in the Experimental Taxonomy Unit of the Zoology Department, British Museum (Natural History). The collectors were D. S. Brown, D. B. Matovu and H. Ndit.

Collector's  
number

- 79–8 Kigoma; marsh crossed by the road to Kigoma airport: *Ferrissia* sp., *Afrogyrus coretus* and *Bulinus forskalii*, from leaves of blue-flowered water-lily, 4 August 1979.
- 79–9 Kigoma; Kirugu dam, situated immediately south-west of Kigoma airfield: *Eupera ferruginea*, *Pila ovata*, *Lymnaea natalensis*, *Biomphalaria pfeifferi*, *Bulinus coulboisi*, from emergent aquatic grass growing on mud, 9 August 1979.
- 79–11 Northern branch of the Malagarasi delta, at ferry-crossing south of Ilagala: *Pila ovata*, *Cleopatra ferruginea*, *Lymnaea natalensis*, *Afrogyrus coretus*, *Segmentorbis angustus*, *Biomphalaria pfeifferi*, *Bulinus forskalii*, from muddy pools beside the main stream, with water-lilies and *Ceratophyllum*, 6 August 1979.
- 79–12 Malagarasi river, main stream about 0.5 km south of 79–11, reached by crossing creek in dug-out canoe: *Gabbiella humerosa tanganyicensis*, *Cleopatra ferruginea*, *Melanoides tuberculata*, from a small residual pool at the upper flood level, 6 August 1979.
- 79–13 Marsh on shore of Lake Tanganyika, north of Ilagala, near the uptake for the town's water supply: *Ceratophallus* sp., *Biomphalaria sudanica*, *Bulinus forskalii*, 6 August 1979.
- 79–14 A large lagoon, about 4 ha. in area, separated from Lake Tanganyika by a ridge of sand, situated below the Regional Hospital at Kigoma; probably the locality that Leloup (1953, p. 17, No. 260) referred to as 'l'étang Bangwé entre Kigoma et Ujiji': *Eupera ferruginea*, *Pila ovata*, *Lymnaea natalensis*, *Segmentorbis angustus*, *Biomphalaria pfeifferi*, *Bulinus coulboisi*, from marginal grass and reeds, 8 August 1979.

- 79-15 Marsh on lake shore at Ujiji, just below the Livingstone memorial monument: *Lymnaea natalensis*, *Afrogyrus coretus*, *Biomphalaria sudanica*, *Bulinus forskalii*, *B. coulboisi*, 10 August 1979.

ADDENDUM

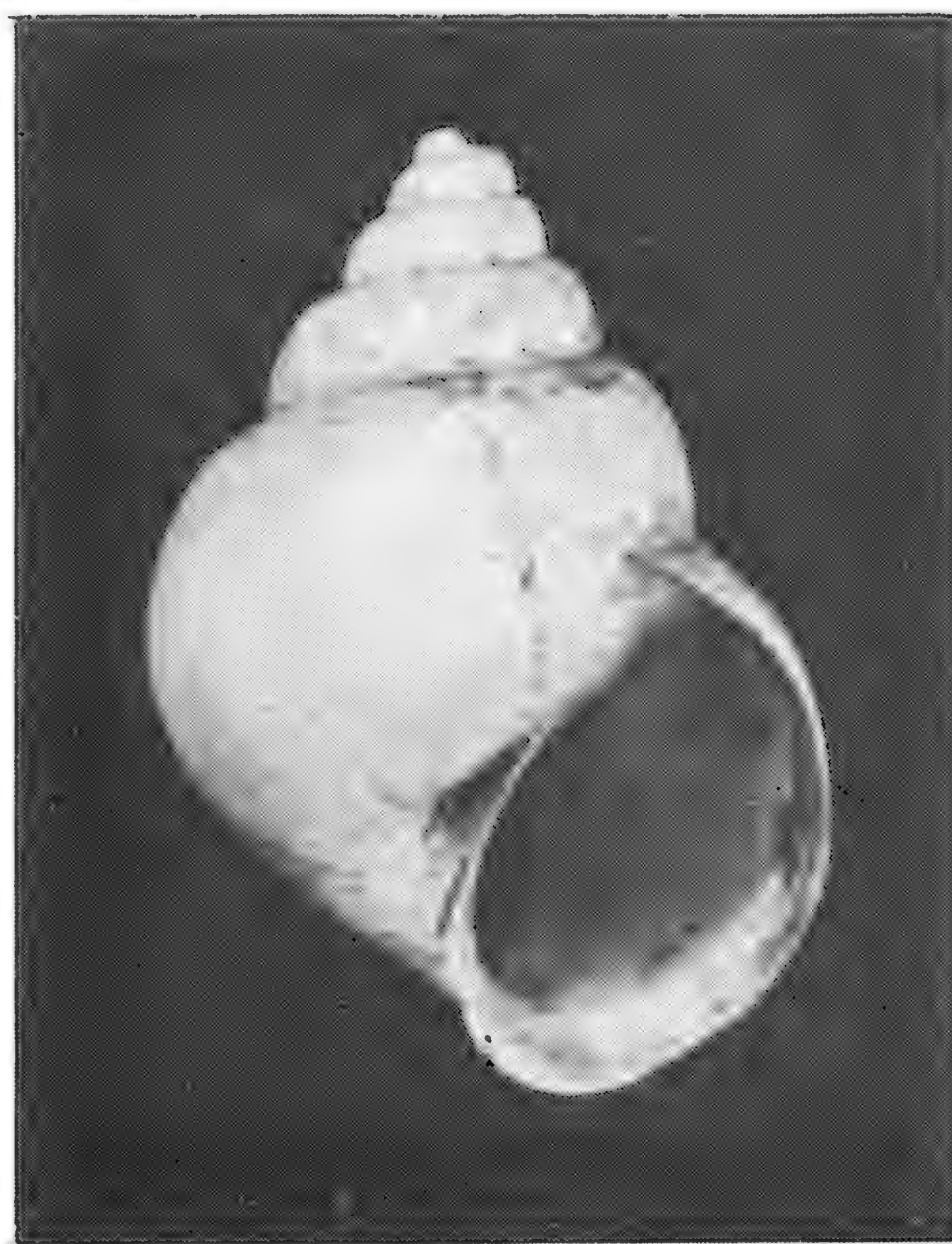
Dr Andrew Cohen (University of Arizona) in conversation with D. S. Brown kindly described investigations by himself and co-workers, currently in progress, that show *Lavigeria nassa* to be, as suggested here, biologically complex. These observations are based on snails collected alive from precisely defined sites, and include multivariate morphometric analysis of the shell, study of breeding cycle and analysis of isoenzymes. Several distinct types of population were recognisable on the Burundi shore, suggesting the existence of a species flock (Johnston, M. R. & Cohen, A. S. In press. Modes of speciation in gastropods from Lake Tanganyika: morphometric evidence. *Palaios*, 2.).



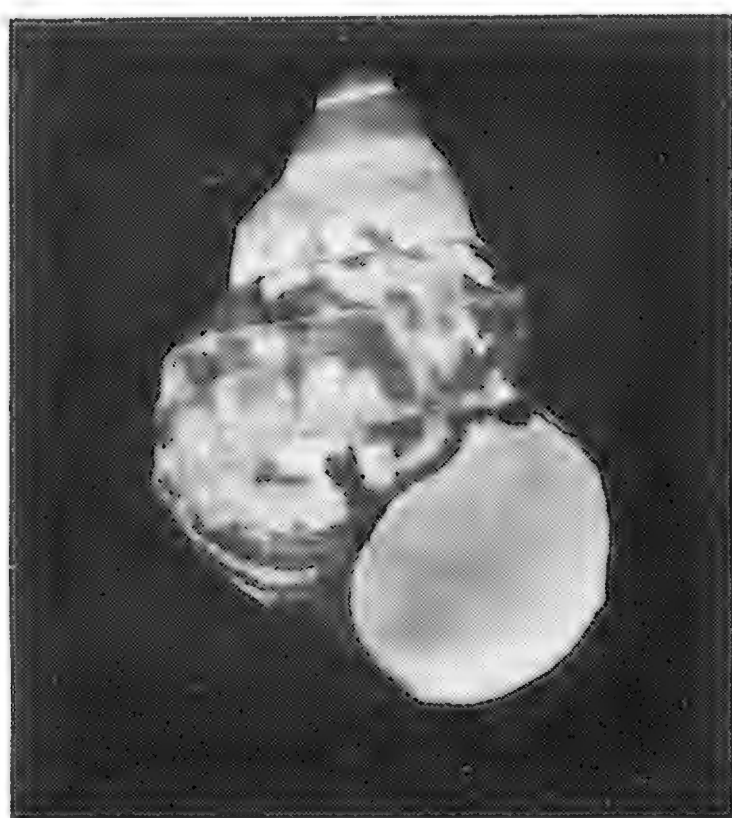




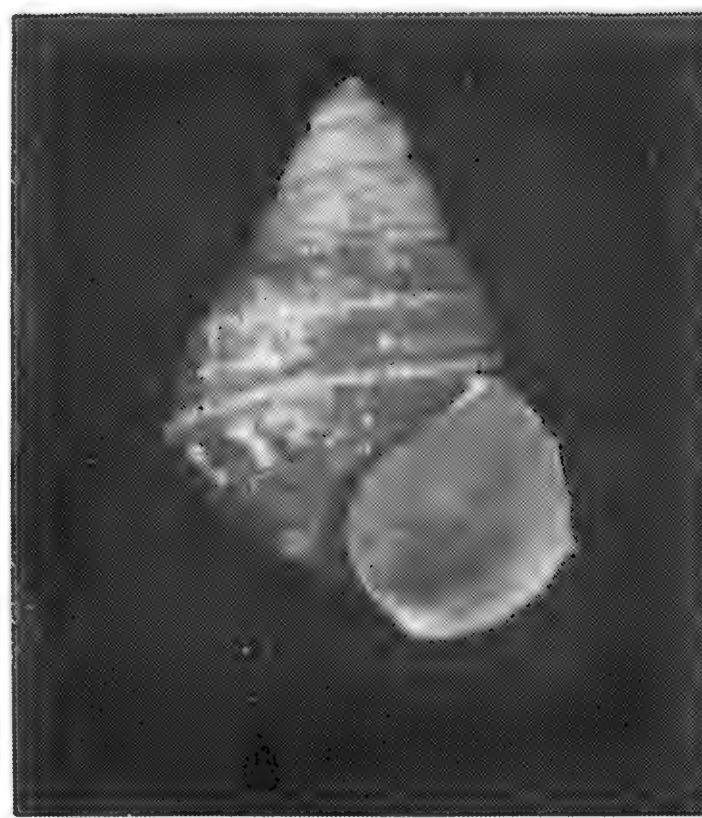
**A**



**B**



**C**



**D**

PLATE 28

A, B, *Cleopatra jouberti* Bourguignat; A, syntype (19.3 mm long) figured by Bourguignat (1888 and 1890, Pl. 4, 3) and B, another syntype.

C, D, *Bellamya trisulcata* (Germain); A, syntype (22 mm long) figured by Germain (1908, Fig. 19–20, as *Cleopatra*) and B, another syntype (Germain 1908, Fig. 21–22, as var. *foai*). Shells in the collection of the Muséum National D'Histoire Naturelle, Paris. The scale lines represent 10 mm.



*ENSIS AMERICANUS* (BINNEY)  
(SYN. *E. DIRECTUS* AUCT. NON CONRAD)  
A RECENT INTRODUCTION FROM ATLANTIC  
NORTH-AMERICA

R. M. VAN URK<sup>1</sup>

(Accepted for publication, 23rd May, 1987)

*Abstract:* The North-American razor-shell *Ensis americanus* was first recorded in the German Bight in 1979, and has subsequently spread westwards along the Dutch coast and northwards up the coast of Denmark. Unlike the European *Ensis* species, it lives in brackish, as well as marine, conditions, and its rapid spread may be partly due to filling a niche not previously occupied. Characters used to distinguish it from European species of *Ensis* are given. This immigrant species, described by previous authors as *E. directus*, is thought to be more properly named *E. americanus* (Binney).

INTRODUCTION

The occurrence of *Ensis americanus* in Europe was recorded for the first time in 1979 from two localities in the German Bight: (1) N. of lightship 'Elbe 1' and (2) Grosser Vogelsand (von Cosel *et al.*, 1982); these are represented in Fig. 1 by the star and the first dot to the south-east, respectively. In the following years the species spread rapidly in both a northern and south-western direction, its present area extending from the northernmost point of Denmark to Hoek van Holland in the Netherlands.

We must assume that the species was transported in the larval stage by a ship containing ballast water, and considering the dimensions of the first European material, this happened not later than the first half of 1978 (von Cosel *et al.* 1982, Mühlenhardt-Siegel *et al.* 1983).

Fig. 1 (after Essink 1986b) shows the rapid extension of its area. It should be carefully read, however, to avoid misinterpretation: '— in 1984 and 1985 the first records of coastal sites outside the Wadden Sea became available. In October and November 1985 shells were found at IJmuiden and Zandvoort-Bloemendaal —. The length of the shells (up to 115 mm) indicates that the species was already present off this coast in 1984, and possibly already in 1983.' Hence 1984 as most southern indication (and 1978 for the first record based upon specimens found in 1979). Subsequently there have been records from Noordwijk, Noordwijk — Katwijk, Scheveningen, and Hoek van Holland (Fig. 2), which show that the species is still on the march.

ECOLOGY

One factor which may be responsible for the rapid spread of the immigrant species relates to its preferred habitats. While the European species all live in the open sea, *E. americanus* frequently inhabits brackish water areas, estuaries etc., thus filling an ecological gap or

<sup>1</sup> Ant. Heinsiusstraat 46, 2582 VV DEN HAAG, Holland.



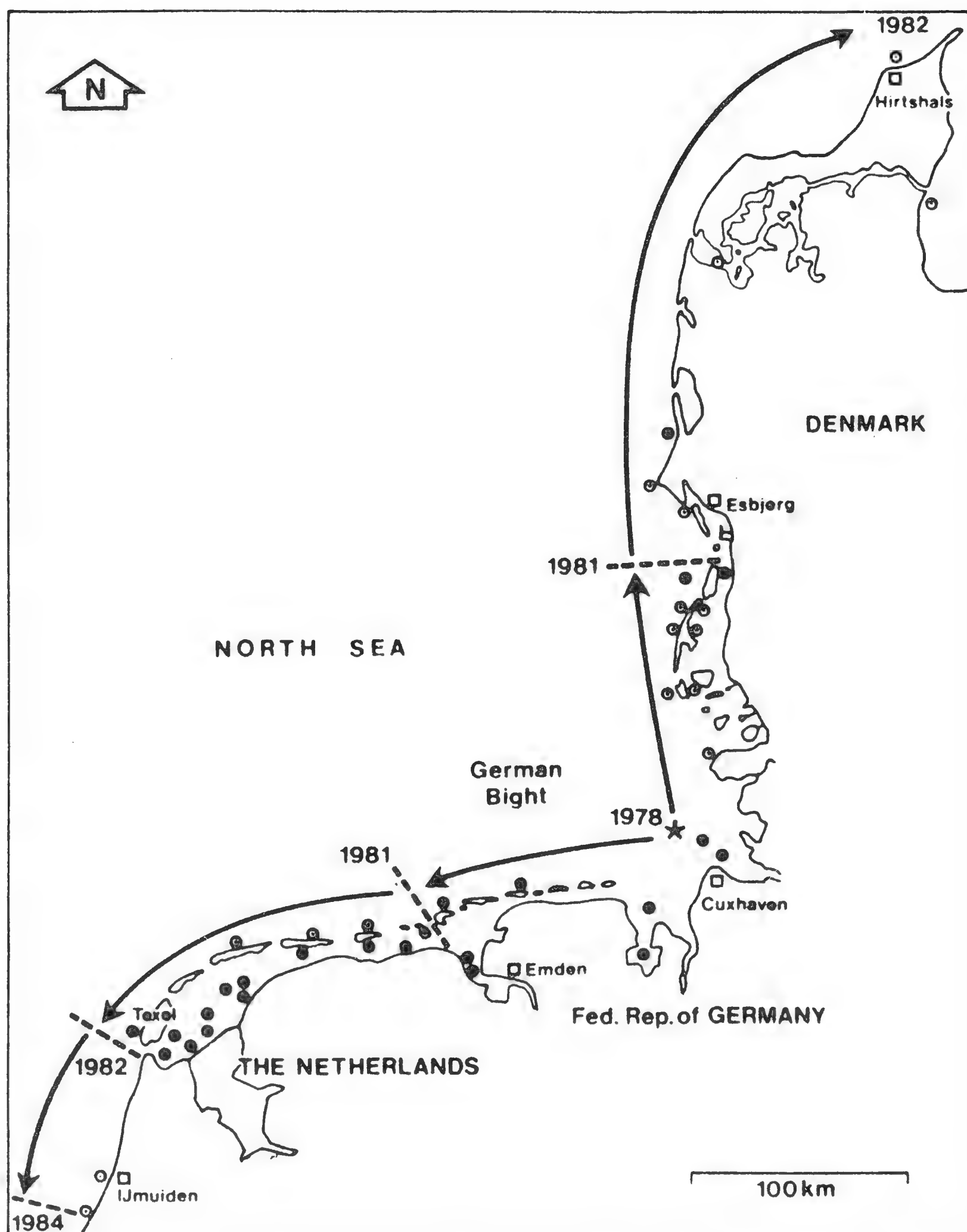


Fig. 1. *Ensis americanus* (Binney) in NW Europe; star = first record, dots = live records, circles = shells washed ashore. (After Essink 1986b).

niche. We do not know if it prefers such habitats or just tolerates the conditions offered by them. Probably, as with *Cerastoderma edule*, it flourishes in these surroundings as well as in the open North Sea, in shallow water below low-tide level. There are no reports of its occurrence in the inter-tidal zone, but they could perhaps be expected.

In the Dutch Wadden Sea, where previously no *Ensis* had ever been found living, it is now well established, occurring with such species as *Mya arenaria*, *Scrobicularia plana*, *Cerastoderma edule*, *Mytilus edulis*, *Littorina littorea*, and *Hydrobia ulvae*. In other parts of its area it is frequently found in similar habitats. 'In 1982 the species was present all over the Dutch-German-Danish Wadden Sea' (Essink 1986b).

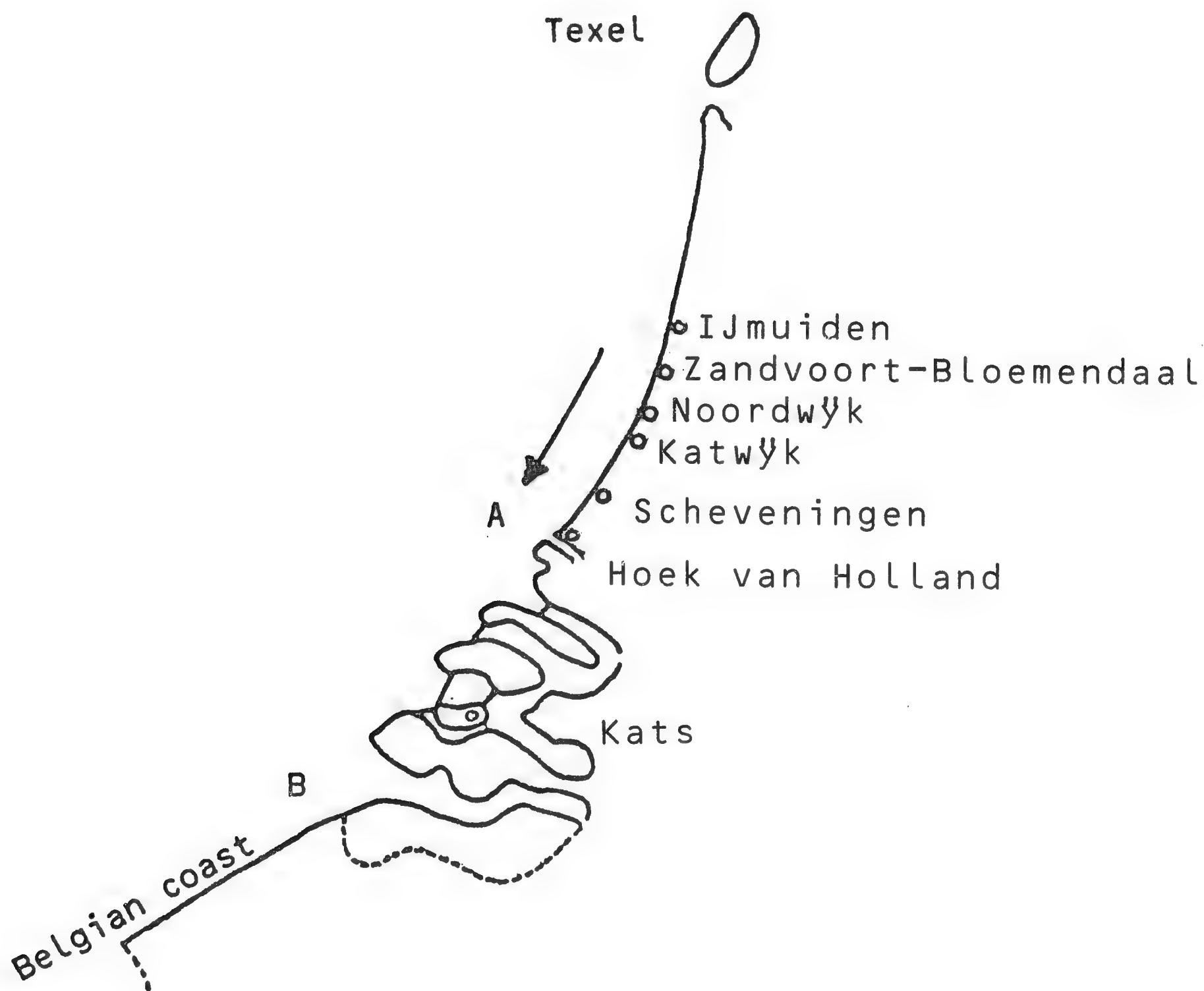


Fig. 2. Recent extension of area (arrow) since Essink (1986b). Approximate distances: Zandvoort-Bloemendaal-Hoek van Holland 55–60 km, A–B, southwestern estuarine area or ‘Delta region’, 90–100 km, Belgian coast 65 km, Scheveningen-Suffolk (Aldeburgh region) 150 km.

#### FUTURE DISPERSAL

The locality Hoek van Holland represents an extension of 55–60 km from the southernmost site on Essink’s map and brings *E. americanus* to the gateway of the southwestern estuarine area or ‘Delta region’. Once there the species is likely to colonize this whole region up to the Zwin at the Netherlands-Belgian frontier.

In a recent paper, Pouwer (1987) mentions empty shells of *E. americanus* from the southern part of the ‘Delta region’: Zandkreek, S. of Kats, on the island of Noord-Beveland. ‘The fact, that they were found on a bed with musselseed indicates their origin. Musselseed is dredged in the Wadden Sea and transported to this region for cultivation’ (free translation).

It seems interesting to note, that here is another way of dispersal, even into unexpected places. Of course larvae could easily use the same way of transport.

The open North Sea coast of Belgium may cause some delay to its progress, but not necessarily for a long time: the similar barrier of the Netherlands coast between the Wadden Sea and the southern estuarine area (the ‘Delta-gebied’ or Delta region) was traversed in a few years only. A species with pelagic larvae, and filling an ecological gap, may be capable of many wanderings.

Any further spread must be more or less a matter of speculation. It may spread further

southwards and then, with prevailing southwestern currents, turn to the British coasts. Or, it could spread straight across the sea, a distance of approximately 150 km at its shortest distance. In any event the Thames estuary seems to provide a suitable or even excellent habitat for the species. In Denmark, where it has been recorded from both the western and eastern sides of northern Jutland, the inner Danish waters may furnish further attractive areas for colonisation.

#### CHARACTERS AND RECOGNITION

Comparing *E. americanus* with the European species of the genus it looks most like *E. arcuatus* (Jeffr.), the following characters serving to distinguish the two species:

<i>E. americanus</i>	<i>E. arcuatus</i>
1. Anterior adductor scar as long as the ligament or slightly longer only.	Anterior adductor scar more than $1\frac{1}{2} \times$ the ligament (var. <i>norvegica</i> : $\pm 1\frac{1}{2} \times$ the ligament).
2. Foot-retractor scar opposite to the insertion marking the end of the ligament.	Foot-retractor scar posterior to the ligament insertion (var. <i>norvegica</i> : opposite to it).
3. Posterior adductor scar very close to the pallial sinus, nearly bordering it.	Posterior adductor scar at about its own length from the pallial sinus.
4. Pallial sinus (often) pointing to posterior adductor scar.	Not so pointing.
5. Length/height ratio 6:1.	Length/height ratio about 8:1.
6. Colour greyish violet with olive green periostracum.	Colour fleshy pink with brown periostracum.
7. Anterior adductor scar (usually) narrowly pointed anteriorly, more or less directed downwards posteriorly.	Anterior adductor scar moderately narrowed anteriorly, slightly directed downwards or almost parallel to the dorsal shell margin.
8. Young specimens: anterior pallial scar markedly closer to the anterior shell margin than the adjacent ventral pallial scar to the ventral shell margin.	Both at about the same distance, or the anterior pallial scar only slightly closer to the anterior shell margin.

The first three of these characters are constant and reliable, revealing the identity of the species at once. The other characters may show more or less variation, but they are useful in different situations, thus for instance the colour (only *E. siliqua* (L.) may show a more or less similar tinge) and l/h ratio when collecting on the beach, or character 8 when dealing with small specimens. *E. arcuatus* var. *norvegica*, a large, broad form of *E. arcuatus*, approaches *E. americanus* in external appearance and the position of the foot-retractor scar (compare 1 & 2), but otherwise its internal characters, and also the colour, are those of *E. arcuatus*.

#### NOMENCLATURE

An extensive study of American Atlantic and American fossil Miocene material – the result of which is still to be published – convinces me now of the fact, that *E. directus* (Conrad), described from Miocene material, is specifically different from the recent Atlantic form, which should be called *E. americanus* (Binney). See also VAN Urk (1964, 1972).

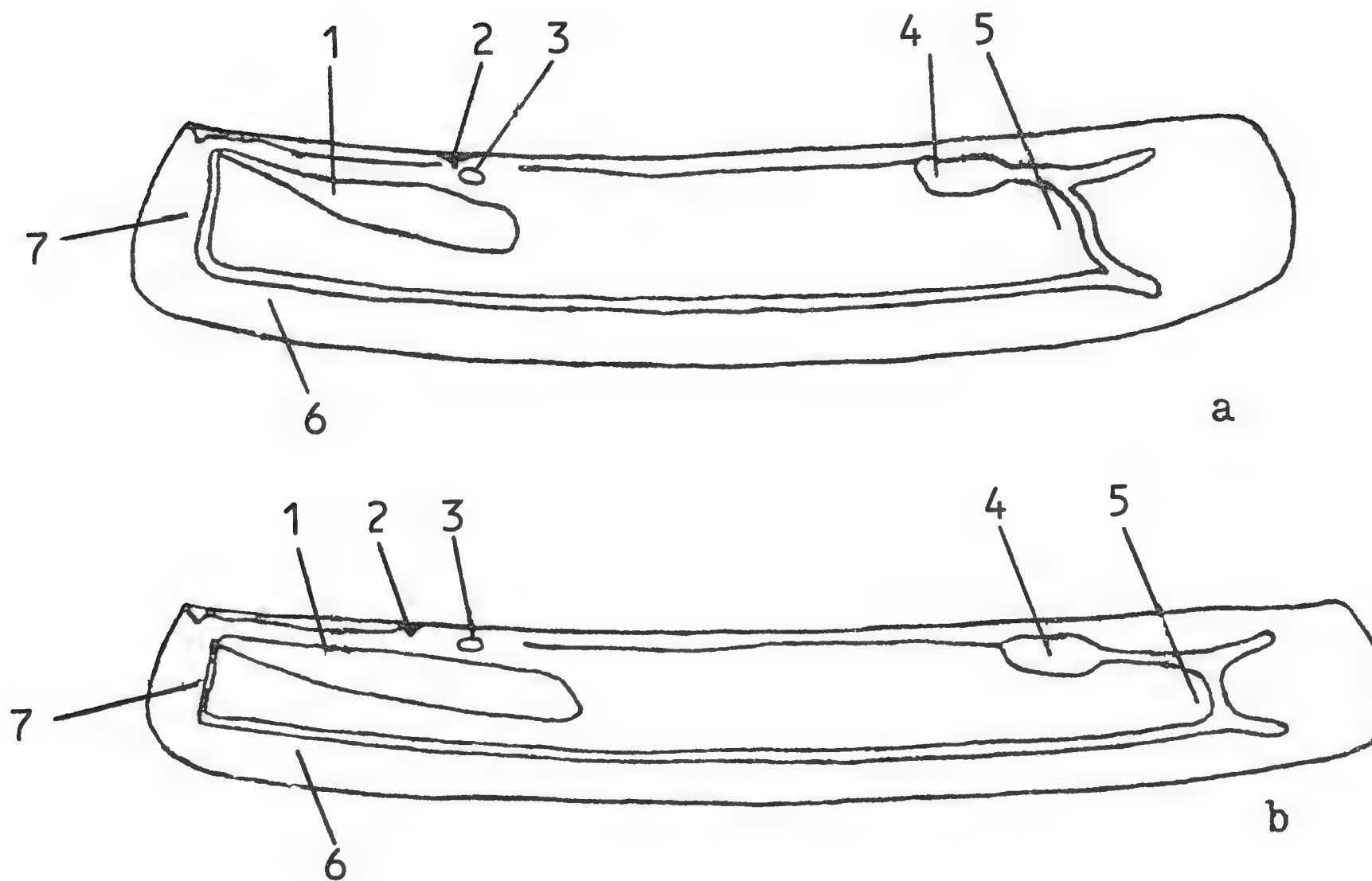


Fig. 3. Interior of a: *Ensis americanus* (Binney), b: *Ensis arcuatus* (Jeffr.) 1=anterior adductor scar 2=ligament insertion (end of the ligament) 3=foot-retractor scar 4=posterior adductor scar 5=pallial sinus 6=ventral pallial scar 7=anterior pallial scar (Also published in: de Boer, 1984)

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# THE CLAUSILIIDAE (GASTROPODA) OF THE MALTESE ISLANDS, SOME ADDITIONAL DATA

K.-H. BECKMANN<sup>1</sup> AND E. GITTENBERGER<sup>2</sup>

(Accepted for publication, 14th February 1987)

**Abstract:** *Lampedusa* (*Muticaria*) *syracusana* from near Syracuse on the island of Sicily is specifically distinct from the polytypic *L. (M.) macrostoma*, occurring on the Maltese Islands. The former species is not known from the Maltese Islands. Most probably the four subspecies of *L. (M.) macrostoma* did evolve from a single ancestral form. To stabilize the nomenclature as good as possible lectotypes are selected for both *Lampedusa* (*Muticaria*) species and some problems with spelling of names and dates of publication are dealt with.

## INTRODUCTION

Interesting papers concerning Maltese Clausiliidae were published recently by Thake (1985) and Holyoak (1986). However, next to presenting valuable new data both authors did not correct a persistent error concerning the occurrence of *Lampedusa* (*Muticaria*) *syracusana* on the Maltese Islands. Caruana Gatto (1892, p. 149) correctly introduced *Clausilia oscitans* var. *pseudosyracusia* as different from the Sicilian *syracusana* after being encouraged to do so by O. Boettger, the well-known specialist in Clausiliidae. For unclear reasons following authors did not accept this view, apart from Nordsieck (1979, p. 257) maybe, who listed two *Muticaria* species (without arguments), viz. *M. scalaris* and *M. syracusana*.

We follow Holyoak (1986, p. 217) in his interpretation of the genus *Lampedusa*, additionally accepting *Muticaria* as a subgenus. As long as clear data concerning the structure of the genitalia of the various forms are not available, we prefer to consider the Sicilian and the Maltese *Lampedusa* (*Muticaria*) specifically distinct. If this view is not accepted, the most important point remains untouched, i.e. that the forms distributed on the Maltese Islands have a diagnostic character in common, which is not shared by the form (at least a subspecies) from Sicily.

## NOMENCLATURE

*Clausilia macrostoma* is generally considered a synonym of *L. (M.) syracusana*. As may be concluded from Sherborn (1928, p. 3775) or Cantraine (1840, 1841, p. 153), the former nominal taxon was published by Cantraine in 1835, with the incorrect spelling *macrosoma*. There is clear evidence in the original publication that ‘*macrosoma*’ is an ‘inadvertent error, such as a . . . printer’s error’ (ICZN Art. 32 (c) (ii)). The epithet *macrosoma* has no relation whatsoever to the diagnosis of the species. The epithet has not been used for any gastropod species during the period 1800–1850 (cf. Sherborn 1928); it does not apply to a particular shell character. On the other hand many authors have used the epithet ‘*macrostoma*’, for species with shells characterized by a large aperture. Most certainly Cantraine intended to be one of them, because the other new species names he introduced refer to diagnostic characters (e.g. *elongata*, *olivacea*, *reflexilabris*, etc.), whereas ‘*apertura* . . .

<sup>1</sup> An der Vogelrute, D 4715 Ascheberg-Herbern, G.F.R.

<sup>2</sup> R.M.N.H., P.O. Box 9517, NL 2300 RA Leiden, The Netherlands.

patula' in his diagnosis of *macrosoma* indicates that a large aperture is considered to be typical for the species in question.

In a small undated pamphlet, apparently overlooked by Sherborn, Cantraine corrected his original spelling into *macrostoma*, repeating his diagnosis. This pamphlet contains articles published before in the *Bulletin de l'Académie Royale des Sciences de Bruxelles* in 1835 and 1836 and, consequently, it has most probably been published in 1836 or afterwards. Finally it should be emphasized that Cantraine's *Malacologie méditerranéenne et littorale, ou . . .* has been published separately in 1840 (as *Extrait du Tom. XIII des Mémoires*) and, rather illogically, in 1841 (as one of the *Mémoires*).

*Clausilia macrostoma* Cantraine, 1835 is described from Syracuse and Malta, which is in agreement with syntypes in the Rijksmuseum van Natuurlijke Historie, Leiden, belonging to two species. There is no need for any action of the International Commission on Zoological Nomenclature and the stability of the nomenclature is not substantially affected if a specimen from Malta is designated as the lectotype, which has been done. Only Caruana Gatto's well-chosen epithet *pseudosyracusia* would have earned better than the graveyard of synonymy.

In addition to Holyoak (1986, p. 219), the following amended synonymy can be given. **Lampedusa (Muticaria) syracusana** (Philippi, 1836); Lectotype (design. nov.): RMNH 55917 (Syracuse; M. J. Landauer, ex Dr. Philippi).

**Lampedusa (Muticaria) m. macrostoma** (Cantraine, 1835); Lectotype (design. nov.): RMNH 55916 (Malta; F. J. Cantraine leg.).

*Clausilia macrosoma* Cantraine, 1835: 381; corrected spelling: *macrostoma*.

*Clausilia macrostoma* Cantraine, 1836?: 3; 1840, 1841: 153, pl. 5 fig. 18.

*Clausilia oscitans* var. *pseudosyracusia* Caruana Gatto, 1892: 149. The original spelling *pseudosyracusia* is used twice and cannot be changed into *pseudosyracusana*; there is no evidence that an inadvertent error is involved.

**L. (M.) m. oscitans** (Charpentier, 1852)

**L. (M.) m. scalaris** (L. Pfeiffer, 1848)

**L. (M.) m. mamotica** (Gulia, 1861)

#### CONCHOLOGICAL CHARACTERS

*L. (M.) syracusana* is very similar to *L. (M.) m. macrostoma* in shape and sculpture of the shell. The inside structure of the aperture, which has the Graciliaria type (Nordsieck 1978, p. 72), is also not clearly different, apart from the upper palatal folds. In both species there is a very prominent, somewhat thickened main palatal lamella, running from the upper part of the lunella towards the apertural lip, which is not reached. Only in the four subspecies of *L. (M.) macrostoma* (Pl. 29, figs. 3–6) this main lamella is accompanied over nearly its entire length by a much thinner but still rather prominent lamella, which can be considered the principalis. In *L. (M.) syracusana* (Pl. 29, figs. 1, 2) the principalis is lacking. In both species there are two more or less obsolete sutural lamellae, which are usually most easily discernible above the lunella. See also Zilch (1977, Pl. 9, figs. 36–39) for additional figures of the shells; the syntype of *pseudosyracusia* (= *macrostoma macrostoma*) (Pl. 9, fig. 38) clearly has a prominent principalis above the main palatal lamella.

#### ZOOGEOGRAPHICAL NOTE

According to Thake (1985, pp. 282, 283) there might have been two invasions of *Lampedusa (Muticaria)* from Sicily to the Maltese Islands during periods in which there has been a

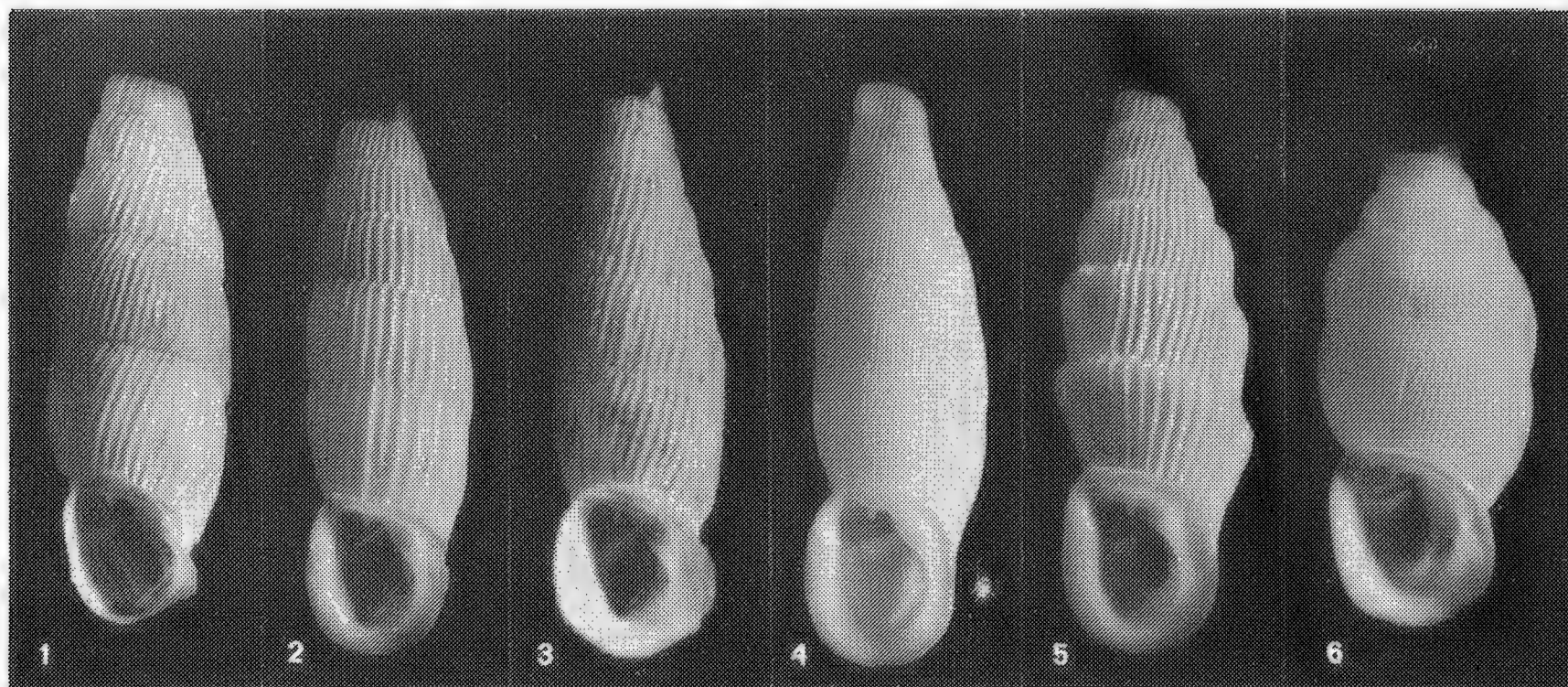


PLATE 29

Figs. 1, 2. *Lampedusa (Muticaria) syracusana* (Philippi). 1, Lectotype, Syracuse (RMNH 55917; M. J. Landauer, ex Dr. Philippi); 2, Syracuse (RMNH; ex Vito Beltrani)

Figs. 3–6. *Lampedusa (Muticaria) macrostoma* (Cantraine). 3, Lectotype, Malta (RMNH 55916; ex F. Cantraine); 4, *L. (M.) m. oscitans* (Charpentier), Malta, N. of Birzebugga, near Ghar Dalam (RMNH; Ph. Pronk leg.); 5, *L. (M.) m. scalaris* (L. Pfeiffer), Malta, St. Pauls Bay – Nistra (RMNH; K.-H. Beckmann leg.); 6, *L. (M.) macrostoma mamotica* (Gulia), Gozo, Munxar – Xlendi valley (RMNH; K.-H. Beckmann leg.). Photographs E. G.; all  $\times 3$ .



land-bridge between these areas. The second, most recent invasion would have resulted in the disjunct distribution of *L. (M.) syracusana*, hybridizing with the endemic *L. (M.) oscitans*, which had evolved in longer isolation in the Maltese archipelago after the first invasion. This scenario, partly based on the incorrect assumption that *L. (M.) syracusana* also occurs on the Maltese Islands, cannot be accepted as probable anymore.

We prefer the alternative hypothesis that the present vicariant species *L. (M.) syracusana* and *L. (M.) macrostoma* evolved from a common ancestor by allopatric speciation. The four subspecies of *L. (M.) macrostoma* evolved most probably on the Maltese Islands by allopatric subspeciation, from an ancestral form with a *principalis* on the palatal wall of the aperture of the shell.

It remains unclear how the present distribution of and interaction between the subspecies should be explained and where exactly their original ranges on the islands have been. This is most problematic for *L. (M.) m. macrostoma* and *L. (M.) m. oscitans* (see Holyoak 1986, Fig. 2).

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# ARION FLAGELLUS COLLINGE AND A. LUSITANICUS MABILLE IN THE BRITISH ISLES: A MORPHOLOGICAL, BIOLOGICAL AND TAXONOMIC INVESTIGATION

STELLA M. DAVIES<sup>1</sup>

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*Abstract:* Two species which were confused by Quick under the name *Arion lusitanicus* are distinguished from each other and from the other British species. Some of their external features, their eggs, the functional morphology of their genitalia, and their mating behaviour, all point to the inclusion of *A. flagellus* in *Mesarion*, and of *A. lusitanicus* in *Arion* s.s.

## INTRODUCTION

In Britain, two distinct species have been confused under the name *Arion lusitanicus* Mabilie. Quick (1952) described in some detail a slug found in and near gardens in Durham, which, although not agreeing exactly with previous descriptions, was not clearly separable from *A. lusitanicus* on the evidence then available to him. Another form was reported by Cain and Williamson (1958), near Nuneaton, but it could not be found again, and no live material was studied or compared with the first form. Quick (1960) has an account of '*A. lusitanicus*' which is based on the Durham slug, but adjusted to include the other.

In 1964, Ellis found the Durham form in Cornwall in August, and another form in Devon in October. He accepted Quick's identification of both as *lusitanicus*, because of the similarity in outline of their genitalia, but he showed his appreciation of their essential difference in his separate accounts: his Cornish slugs 'struck one at first sight as being different from *A. ater* (L.)' (Ellis 1964, p. 285), but the Devon slugs 'were virtually indistinguishable from some colour forms of *Arion ater* (L.) and *A. rufus*' (Ellis 1965, p. 345). He recognised both forms among the new finds recorded in the next few years as *A. lusitanicus*, and commented 'There seem to be two distinct races' (Ellis 1969, p. 267).

Most of the British records of '*A. lusitanicus*' have now been assigned to the two species, identified as *A. flagellus* Collinge and *A. lusitanicus* Mabilie. Since it has not been possible to investigate every record, some may remain, unassigned, as '*A. lusitanicus* s.l.', but there is no need to postulate for these any '*lusitanicus* complex', and such a designation would be quite inappropriate. *A. flagellus* is more closely allied to *A. subfuscus*, which is the type species of the subgenus *Mesarion*, but *A. lusitanicus* belongs to the *A. ater* complex, subgenus *Arion* s.s., also known as *A. ater* agg., *A. rufus* agg., or the *A. empiricorum* complex (Chevallier 1981).

## RECOGNITION OF THE BRITISH SPECIES

The Durham slug, *Arion lusitanicus* Quick, non Mabilie, according to Quick (1952, p. 94) 'resembles *ater* in the following features: large tubercles, mantle bands comparatively

<sup>1</sup> 63 Beechwood Road, South Croydon, Surrey CR2 0AE.

near each other anteriorly, colour range, black head and tentacles and capacity to assume a hemispherical shape when contracted. It resembles *subfuscus* in foot fringe, pale sole even in dark individuals, relative size of respiratory orifice, lower genital ducts, eggs and date of egg laying'.

These features have now been studied in slugs from many British localities, and Quick's observations are confirmed in general for *flagellus*. While the essential unity of each species is more clearly seen in details of copulation, and in the morphology of the spermatophore, some more variable characters are also found to be useful in identification, at least locally.

*1. Tubercles.* Typically, the dorsal tubercles of *flagellus* (= Durham slug) are about twice as widely spaced as are those of British *subfuscus*, and intermediate conditions prevail in the *ater* complex, which includes *lusitanicus*. The difference between adult *flagellus* and *ater* may be quite striking, or more obscure, depending much on the size and physical condition of the animals. In British *lusitanicus*, the tubercles tend to be rather more regular and less prominent than in either *flagellus* or *ater* at a comparable stage.

Clearer and more consistent differences are found in juvenile slugs with well-defined pigment bands. Counted across, just behind the mantle, the number of dorsal tubercles between, and not invaded by, the lateral pigment bands, is: in *flagellus*, usually no more than 7 or 8, but occasionally up to 10; in the *ater* complex, including *lusitanicus*, usually at least 9 or 10; and in British *subfuscus*, at least 12, sometimes up to 19.

*2. Banding.* No species has an absolutely invariable pattern, but some features may be very constant in local strains, and then valuable (locally) in the identification of juveniles.

The anterior approximation of the mantle bands is often very strongly marked in *ater*, particularly in Scotland, and generally less well marked in *lusitanicus*. The mantle bands of *flagellus*, however, are usually much more widely separated, more like *subfuscus*, and less like *ater* than was suggested by Quick.

The pattern at the posterior edge of the mantle may be indicative. From their first appearance in hatchlings, the mantle and body bands in both *flagellus* and *subfuscus* meet, almost, if not quite, end to end, even when the slug is contracted; but in the *ater* complex the upper edges of the body bands tend to transgress the rows of tubercles anteriorly, so as to end below the lower edges of the mantle bands, and if the bands are narrow they may not quite meet, even when the slug is fully extended.

*3. Colour.* In *flagellus*, as in the *ater* complex, there is a wide range of colour. Some populations show only one adult colour, but black, brown, and purple, of varying intensity, are all found in *flagellus* at Durham. The more lightly pigmented individuals are usually yellowish, or greenish, and may retain traces of the juvenile banding. Very often, the first sign by which *flagellus* is recognised, or suspected, is a peculiar green background tint. This green usually appears at a very early stage, and it may still be just discernible in the more translucent areas of the sole, and the furrows, of even a black adult. It also contributes to the strikingly colourful transitional stages which are characteristic of *flagellus*, when the adult pigment is spreading, and the dorsal tubercles are still capped with rusty orange and separated by conspicuous greenish furrows.

The other species normally show only two main colours, yellow or orange, with brown or black, in addition to some whitish areas. Strongly banded juvenile *lusitanicus* were found throughout the Exeter district in May 1979, and these were all either yellow or orange, with black bands, as were most of those found at Torquay. In Brunel Woods, near Torquay, there were also a few plain yellow, unbanded, individuals, resembling juvenile *ater*, but their heads and tentacles also lacked pigment, and they developed into mature *lusitanicus* which were virtually albino. Different variations in the pigmentation seem to be characteristic of different populations of *lusitanicus*. The sub-adult *lusitanicus* often retain a clear orange stripe immediately above the original dark band, and sometimes, e.g. at Glasgow, the entire dorsum may be orange while the flanks are black. Adult *lusitanicus* can



often be roughly described as rusty black, or brown, the whole body, including the sole, having a more or less densely pigmented black underlayer, beneath a slight, or thick, sprinkling of orange pigment. The black layer appears to be deeper than in *ater*, as superficially damaged brown or orange *lusitanicus* may show black wounds, where a similarly damaged black *ater* would show white wounds. In the blackest *lusitanicus*, found in Hawkhurst, the orange covering is reduced to a trace of light yellow, which gives a dull greenish effect on the black surface, but this should not be confused with the greenish background tint already described in black *flagellus*.

A pale sole, even in dark individuals, is a feature which *flagellus* shares with *subfuscus*, as Quick observed, and no exceptions have been found. Before *flagellus* was recognised, it could have been passed over as immature *ater*, especially when black, but it can be distinguished by its rather less well developed foot fringe, and more abrupt ending of the pigmentation at the very edge, as well as by the green tint already mentioned. In British *lusitanicus*, the sole varies as in *ater*, and is often darker than the body. Its lateral areas sometimes have black transverse lines on a dark grey ground, not the creamy ground which is common in some British *rufus*.

The head and tentacles are usually black in *flagellus*, as in the *ater* complex, but are often tinged with violet or purple. In British *subfuscus* the tentacles are usually paler, and pinkish or brown, but grey in some strains. Tentacle colour can be very useful in field identification, locally, because it persists, without significant change, from hatchling to adult. The dark pigment may increase, but an outstretched adult tentacle will still show a pink or purple tint if this was present in the hatchling.

In order to assess the often-quoted resemblance of juvenile *lusitanicus* to *subfuscus*, broods of the two species have been raised and observed side by side. The general orange-brown body colour often matched perfectly, and differences in pattern were not obvious as the slugs' sizes and postures varied, but the dark heads of the *lusitanicus* and the paler heads and pinkish tentacles of the *subfuscus* always made the two species easily separable at a glance.

In *flagellus*, and *lusitanicus*, as in *ater* and *rufus*, pigmentation of the mature genitalia sometimes occurs, subject to individual variation. Black pigment is found more commonly, but not invariably, in darker slugs, and a purple colour sometimes replaces the black in *flagellus* when the tentacles are purple, e.g. at Croydon.

4. *Shape, respiratory orifice, and swaying motion.* A capacity to contract to a more or less hemispherical shape may be shown by *flagellus*, and sometimes even by *subfuscus*, as well as by the *ater* complex. Immature *flagellus* however, when contracted on a more or less circular base, tends to be lower than a hemisphere, while *ater* and *subfuscus* are often markedly higher. Some populations do appear to have characteristic shapes and attitudes, but these vary greatly with development stages, and with physical conditions.

The extremely marked degree of dilation of the respiratory orifice, which Quick regarded as indicative of *ater*, appears to be similarly uncertain. It must be at least partly size-related, and a well-grown or overgrown *flagellus*, or even *subfuscus*, may sometimes show a comparable dilation, especially during mating.

More characteristic of a population, although not of a whole species, is the curious habit of swaying and twisting the contracted body, rhythmically, in response to some disturbance. This has not been observed in either *flagellus* or *subfuscus*, and it appears to be peculiar to the *ater* complex, but it has not been adequately recorded. The response has been very regularly and readily obtained in Scottish *ater*, even from quite small juveniles, and Scharff (1891) reported the same in Irish *ater*. Quick (1947) recorded it in both *ater* and *rufus*, 'after becoming nearly full grown'. However, English populations vary quite markedly; while *ater ater* often responds in this way immediately on being handled, *ater rufus* generally needs considerably more provocation. The same rocking motion has also been seen in *lusitanicus*, but only in a very well-grown, and somewhat senile, individual.



5. *Eggs*. Typical eggs of *flagellus* measure no more than about 3 mm in diameter, and exactly resemble the eggs of *subfuscus*. They are laid in coherent clusters, and captive slugs often attach their clusters to the lid or side of a container. The eggs of *lusitanicus* are usually at least 4 mm in diameter, and exactly like those of *ater*. They are laid in the soil, often under stones in the garden, in clusters which readily fall apart.

The appearance of typical clusters of eggs is sufficiently striking to suggest, or confirm, a close affinity between *flagellus* and *subfuscus*, as well as the inclusion of *lusitanicus* in the *ater* complex. However, the distinctions are not absolute: the eggs vary in size and shape, and all become similarly opaque and chalky.

6. *Spermatophore*. A distinctive form of spermatophore must indicate the reproductive isolation of a good species. Quick (1952, 1960) described and figured a spermatophore of the Durham slug. A virtually identical spermatophore has been obtained many times from *flagellus* taken from Durham, Glasgow, Cornwall, the Wirral, and Croydon. These slugs have mated readily in captivity, and have interbred. The fresh spermatophore is flexible and elastic, tending to retain characteristic curves – see Fig. 1A. Note that the curvature is 3-dimensional, and the longitudinal ridge, following the convex edge of the curve, gives a clue to the correct interpretation of the drawing, which shows a specimen resting centrally and at each end on a plane surface. The form of Quick's drawing suggests that his only specimen was unnaturally straightened and somewhat flattened. It was probably damaged when it was sent to him, in formalin. He also saw 'two low smooth ridges at the posterior end', which have not been found again, but this region can split longitudinally when damaged. The denticulations of the longitudinal ridge are rather fine and regular, and considerably more pronounced than any yet seen in *subfuscus*.

The spermatophore of *lusitanicus* has been obtained from the Glasgow Necropolis, from Okehampton Park in Devon, and many times from Sanderstead and South Croydon. It is larger than the spermatophore of *flagellus*, often about 27 mm. long, with a fragile filamentous tail of indefinite length (Fig. 1B). It is distinguished, even in fragments, by the very regular width and curvature of the anterior portion, and by the exceptionally large and strongly pointed denticulations of the longitudinal ridge, which continue almost to the anterior tip.

Quick (1947) described and figured and spermatophores of British *ater* and *rufus*, and fresh specimens from both forms have confirmed his description. They are similar in size, or rather smaller than the *lusitanicus* spermatophores, much straighter in the anterior half, enlarging gradually to their maximum width in the posterior half – (Fig. 1C). The longitudinal ridge has much smaller and more numerous serrations, and these are irregularly grouped near the anterior end.

The significance of the strongly serrated ridge, which is so well developed on the wider portion of the larger arionid spermatophores, is that it gives great strength with controlled flexibility. Even if the forward-pointing teeth may help to hold a spermatophore while it is being prepared and filled, they in no way impede its progress after it has been released. The points also curve slightly over to their left, making the actual edge of the ridge smooth rather than sharp, and they are embedded in a very thick and tough coat of mucus which is carried forward with the spermatophore, enabling it to pass smoothly, in less than 24 hours, from the position indicated in Fig. 3J to that shown in Fig. 3H.

7. *Genitalia*. If each variable species of *Arion* is characterised by the possession of a distinctive, and much less variable, spermatophore, then the organs concerned in the production and exchange of spermatophores must be of considerable taxonomic importance. Unfortunately, the form of the spermatophore is not accurately indicated by an epiphallus which is not both fully mature and fully turgid; and all soft parts are modified, not only by growth and development, but also by distortions which occur naturally in life, at death, and in dissection. The general similarity in basic plan of the

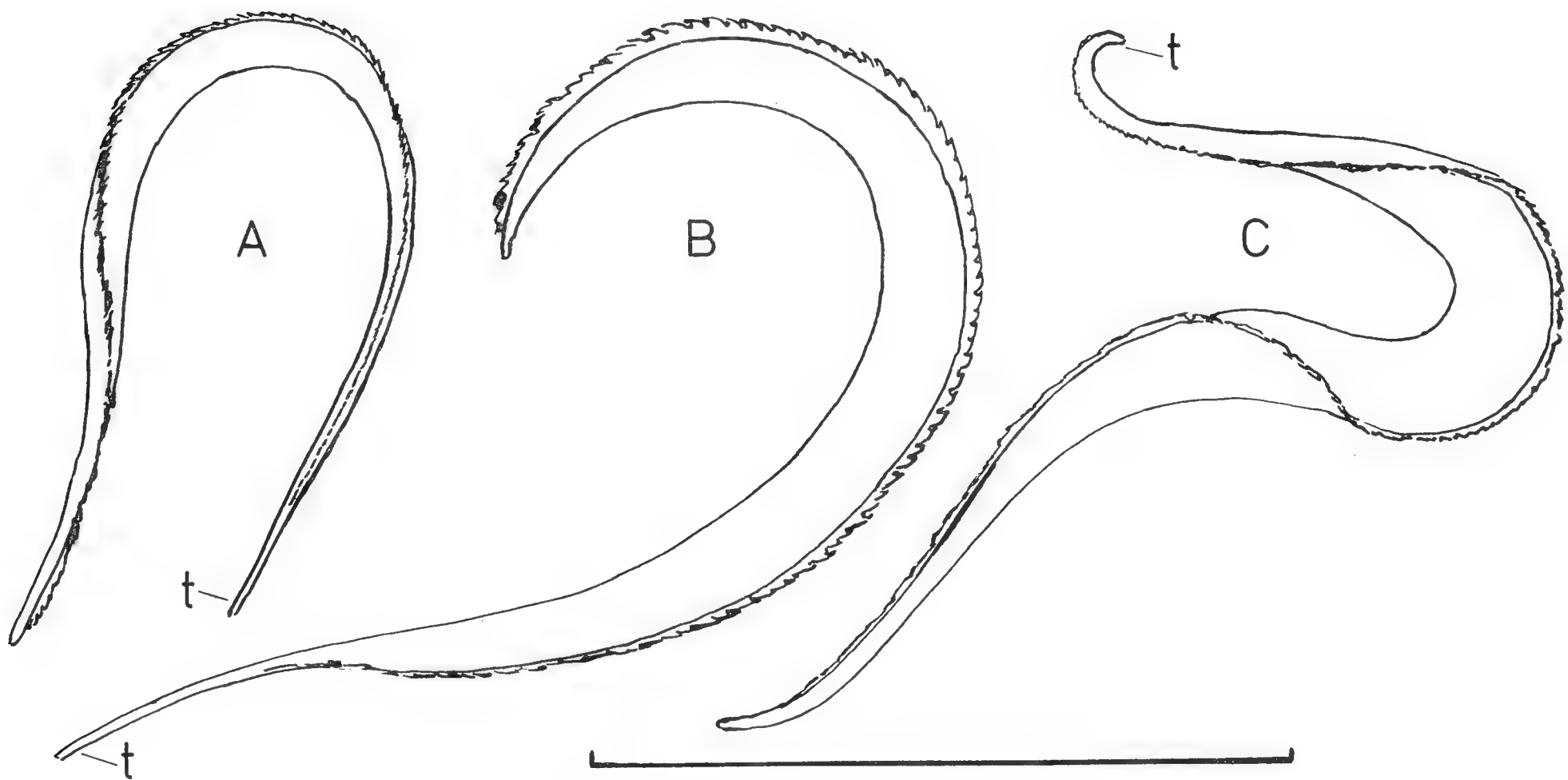


Fig. 1. Spermatophores.

A. *Arion flagellus* – Durham. B. *A. lusitanicus* – Glasgow. C. *A. ater* – Croydon. t = tail.

Scale bar = 10 mm

genital anatomy has therefore been sufficient to allow *flagellus* to be mistaken for *lusitanicus*, as well as being confused with *subfuscus*.

Ellis (1964, 1965) mentioned as a characteristic feature of *lusitanicus* ‘a dilatation about the middle of the rather short spermatheca duct’, which was more pronounced in his Cornish specimens, i.e. in *flagellus*. Such a dilatation may be found, or produced by manipulation, in both species, but its position and extent are not very constant in either. It represents a strengthening of the bursal duct at the attachment of its retractor muscle, which is where the newly inserted spermatophore is most tightly gripped when the slugs separate after coitus.

The posterior genital retractors are seen in a fairly relaxed condition, after copulation, in Figs 2L and 3H. In both species some variation is found in the apparent degree of fusion or separation of the branches at their origin, and in the position and extent of the attachment of each branch to the oviduct or to the bursal duct.

Specific differences in the position and proportions of muscles, ducts and organs cannot always be easily recognised because such details are to some extent size-related, as well as age-related. In large slugs, like the *flagellus* of Fig 2L and the *lusitanicus* of Fig. 3H, the organs are much less crowded than they are in a smaller slug like that of Fig. 3J, which contains a spermatophore of the same size as that in Fig. 3H. The distension of the organs by a spermatophore shows its position before it has been uncovered by further dissection. Fig. 3K shows the appearance of the organs in a rather small and senile *lusitanicus* which is almost choked by the presence of five fully formed eggs.

The oviducal bulge is a conspicuous feature of *subfuscus*, *flagellus* and *lusitanicus*, even when very immature, and it is clearly subject to change and distortion, as well as variation. Its significance is seen in copulation, when it is everted and enormously distended, after which it accommodates the tail of the spermatophore, folded back on itself or coiled if necessary. In a dissection, the bulge may be likened to a collapsed balloon, inside out, in that its functional form and detailed structure are not immediately apparent. It contains an important structure known as the ligula, which, when unfolded and extended in copulation, may be applied to the ground or to some opposing surface of the slug’s partner. In

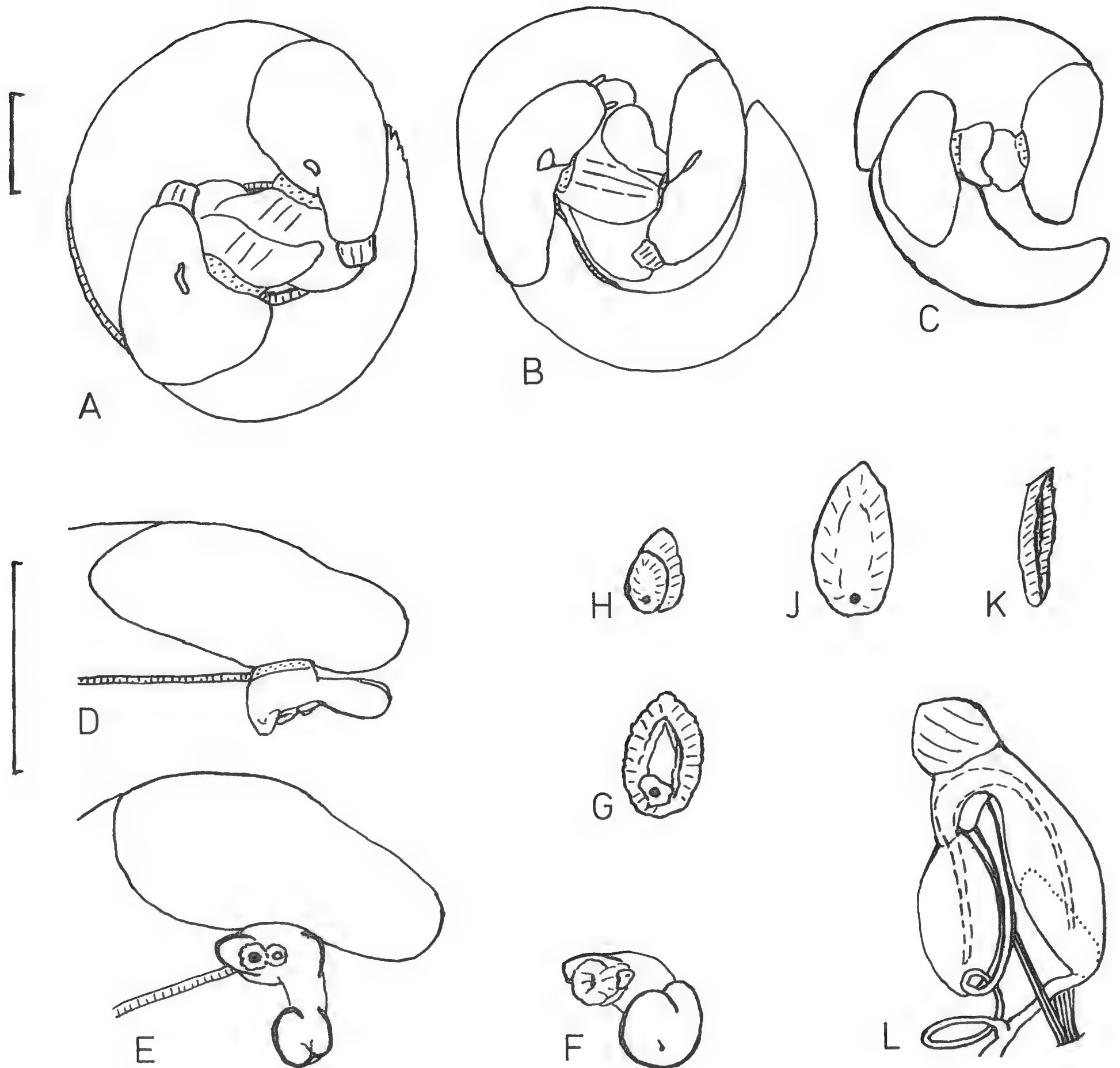


Fig. 2. *Arion* (*Mesarion*) *flagellus*.

A,B. Copulation: outline sketches from life. C. The pair B when frozen solid. D. Specimen with exserted genitalia in dorsal view, with the ligula face down and hidden beneath the oviducal bulge. Note the prominent posterior lip, over the bursal duct, which features conspicuously in A and B. E,F. Similar specimens in lateral view, with the ligula hanging down and turned to face outwards. G,H,J. The ligula in other examples, opened out, nearly fresh, but slightly wrinkled. K. The ligula J, as seen folded together in L. L. Genitalia, only slightly shifted, in a slug opened from below. Dotted line = area occupied by the ligula J,K. Broken line = position of spermatophore in bursal sac and duct, with tail in the ligula sac, or oviducal bulge. Scale bars = 10 mm.

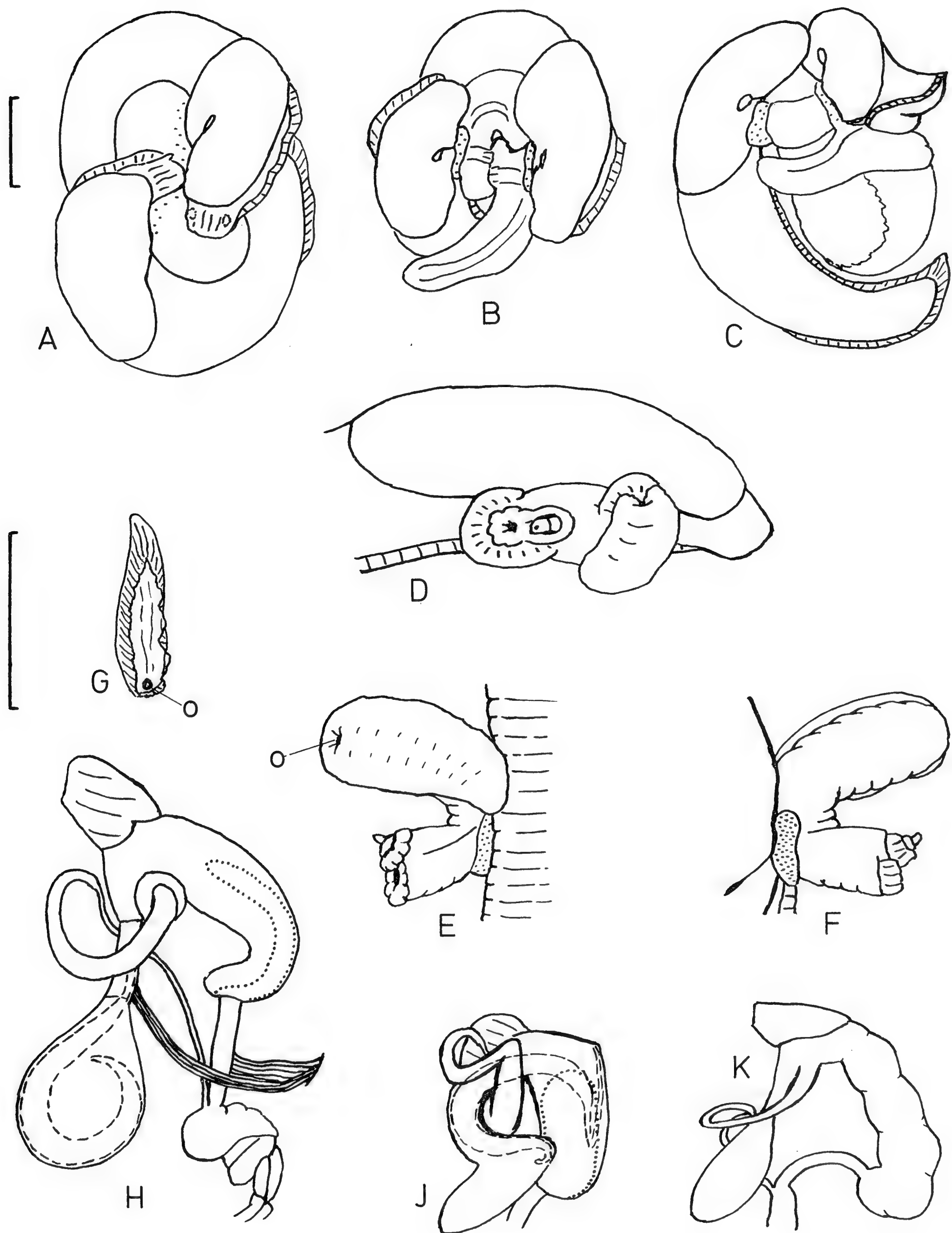


Fig. 3. *Arion (Arion) lusitanicus*.

A,B,C. Copulation: outline sketches from life. A, with head movements – Glasgow, B,C, with movement only in the exserted genitalia – Sanderstead. D. Specimen with eversions partly contracted, but the ligula only just begun to withdraw. E,F. Ventral and dorsal views of a similar specimen, its ligula facing downwards and pulled out to show the oviducal orifice (o). G. Typical boat-shaped folded ligula from dissection. H. Genitalia in very large slug, dissected from below. Dotted line = base of the ligula G. The spermatophore (broken outline) in the bursal sac was probably received some 20 hours earlier. J. Same organs in a small slug with a newly received spermatophore. K. Same organs in a senile egg-bound slug. Scale bars = 10 mm.



stabilising the pair, and perhaps in stimulating the mating process, the position and movements of the ligula may be more important than its very changeable shape and size.

The ligula of *flagellus*, like that of *subfuscus*, is basically a rounded pad which surrounds and conceals the oviducal orifice at the termination of the exerted oviducal bulge. It is not visible during copulation, when the bulge is fully distended, but in a relaxed specimen where it has been exerted, either by the dying slug or by subsequent manipulation, the ligula is found facing more or less downward, but able to twist round (Figs. 2D, E, F). It measures about 3 mm to 7 mm, and it is smooth and featureless when fresh and covered in mucus. The outline of the ligula sometimes appears to be broken, and connected with a more or less thickened fold continuing back to the dorsal part of the atrium (Fig. 2E), but more often the edging fold tends to duplicate (Fig. 2F). Inner folds, parallel to the edge, or surrounding the oviducal orifice (Figs. 2G, H) often become apparent as the specimen begins to shrink. The ligula, whose normal position is indicated in Fig. 2L, is found folded lengthwise as in Fig. 2K, to appear as Fig. 2J when opened out. In spirit material, the edges, and any major internal folds, are usually pleated like frills, and the whole surface may be thrown up into small folds, or papillae, with no constant configuration.

The ligula of *lusitanicus* has a firmer and more fleshy base, with a greater tendency to make a right angle at the entry of the oviduct, as Ellis (1965) observed. If the bulge is pigmented, the base of the ligula appears as an unpigmented area (Figs. 3H, J), just as it does in *ater* and *rufus*, as well as *flagellus*. Pigmentation sometimes extends over the outer side, or back, of the ligula, but not its inner side, or face. Typically, the contracted ligula in British *lusitanicus* forms a characteristic long boat or slipper shape (Fig. 3G), which may measure up to about 24 mm in a dissection, and can also be recognised from an early stage, even at less than 1 mm. Its edges, which spread out, on exertion, like the fringe of a footsole (Figs. 3E, F) are unevenly developed, and are usually reduced near the oviducal end and on the side which remains proximal in exertion. Whatever the shape of the ligula in *lusitanicus*, the oviducal orifice is always situated at the end which is last to emerge and first to withdraw, not centrally or towards the other end as it is in the ligula of British *ater* and *rufus*.

*8. Mating and seasonality.* Quick was unable to describe mating in either *flagellus* or *lusitanicus*. With captive *flagellus*, as with *subfuscus*, observations can be made quite easily when separately confined individuals are put together at a suitable stage in their development. A pair may then mate normally within a few hours, but sometimes, after the usual preliminary period of following, they merely remain encircled, with their genital apertures opposed, either motionless or slowly rotating, for up to an hour, and then separate without achieving copulation: this may be because they are not quite ready, and the same pair will mate without delay at a second attempt within the next few days. The duration of actual coitus, timed from the rather sudden full eversion of the genitalia, is in a range very similar to that found in British *subfuscus*, e.g., 85 to 87 minutes on several occasions, 125 minutes, and, only once, more than 160 minutes. There is usually some nibbling and slow rotation at first, followed by a longer motionless period with the tentacles completely withdrawn, and further activity shortly before separation. In *subfuscus* the exerted organs tend to pile up over the small space between the animals, as noticed by Quick (1946), but in *flagellus* the greater bulk is always below, and it is possible, in the later stages at least, to discern, from above, the opaque ducts lying beneath the translucent posterior lips of the atria, as indicated by the straight lines in the middle of Figs. 2A and 2B. All that can be seen of the oviducal exertion is the smooth round bulge beneath each slug's head: the terminal part, with the ligula, is apparently thrust down into the cushion of gelatinous mucus on the ground.

Captive *lusitanicus* rarely attempt to mate, but one pair from Glasgow succeeded, after several abortive attempts. This pair finally became encircled together for a total of 4 hours, with full eversion lasting for 215 minutes, during which there were several periods of movement, when the animals rotated slowly, with heads and tentacles partly extended. One

of these slugs was dissected immediately, for the spermatophore, but the other, although well-grown and apparently healthy, failed to lay eggs, and died egg-bound some 4 months later.

In 1981, the first season after the arrival of the species had been noticed in Sanderstead, matings of *lusitanicus* were frequently observed. On almost any fine night, soon after sunset, from late July until early September, the slugs could be seen pairing in the garden, on paths and bare ground, on the lawn, on the rockery, and on the compost heap. In every case where the whole procedure was observed, full coitus lasted for 140 to 150 minutes, and the slugs always lay quite motionless until the last 5 to 10 minutes. Usually the closeness of the slugs' heads hid any detail that might distinguish them from *ater* or *rufus*, and the bulges visible from above were often smaller than in the Glasgow pair shown in Fig. 3A. The effect of any pigmentation is greatly reduced by the stretching of the organs, and the bulges always appeared conspicuously pale, and glistening, in moonlight or torchlight. The eversions shrank and withdrew just before the animals separated, when the projecting tails of the spermatophores identified them as *lusitanicus*. If a pair was disturbed earlier, the oviducal exsertions disappeared before they could be examined. One pair was found, however, showing the oviducts quite clearly in an anterior and dorsal position – Fig. 3B. Another pair, when lifted very gently, showed not only the oviducal end of the ligula in a dorsal position, but also the greatly expanded edge of the lower part making tiny rippling movements over the surface of a large spheroidal mass – Fig. 3C. Here, at full eversion, the entire face of the ligula was applied to the partner, and adhesion to the ground was reduced to a minimum by the raising of the slugs' bodies.

The mating season of *lusitanicus*, which was so conspicuous in 1981, was much less active in 1982, and signs of pairing have not been obvious in subsequent years, although the garden population has scarcely declined. Large numbers of eggs are laid every autumn, and the adults have usually disappeared by the end of November.

In the south of England, both *flagellus* and *lusitanicus* appear to be mainly annual, with *flagellus* maturing rather later in the year than *lusitanicus* and laying its eggs well into the winter. Alteration and extension of the breeding season may be achieved in *flagellus* by more rapid development in favourable conditions, as in the laboratory animals from Durham described by Quick (1952, 1960), but *lusitanicus*, like *ater*, tends to produce individuals, if not populations, in which maturity is not attained until the second year. This delay in the development of some individuals, and not others from the same brood, has been observed in broods raised from eggs, or collected as small juveniles, from localities in Devon and Kent, as well as Sanderstead. In the field, juvenile *lusitanicus* of all sizes may be found in the winter, the largest of them presumably being in their second winter. These may result in exceptionally large adults, which are sometimes found stretching to 15 cm, and weighing as much as 25 g by the end of June. It is possible that the *lusitanicus* at Glasgow may be normally biennial.

#### SUMMARY: COMPARISON OF *A. FLAGELLUS* AND *A. LUSITANICUS* IN BRITAIN

The most constant feature of each species is the morphology of its spermatophore (Fig. 1), but this is not usually accessible. Other characters become more difficult to recognise when development is not uniform or predictable, and their variability tends to increase with the age and size of the slugs. Adult *flagellus* is sometimes found measuring no more than 3 cm, while 7 to 10 cm is common, and 10 to 12 cm not unusual. Adult *lusitanicus* ranges from less than 4 cm to a more usual 10 to 12 cm, and an occasional 12 to 15 cm.

*A. flagellus* is easily recognised in its juvenile stages by the continuity of the banding pattern, and by the comparatively few, widely spaced, dorsal tubercles, from which it derives a more or less distinctive adult appearance. It has an invariably pale sole, and, nearly always,

a peculiar green background tint. A slug which has not been recognised with certainty in the field will often reveal its specific identity within a few days of capture, by acquiring a more definite green tint, or by recovering a more typical shape in better conditions. Sometimes it may do so after laying eggs, which strongly resemble the eggs of *subfuscus*. Internally, *flagellus* resembles *subfuscus* in essentials. The ligula is usually well developed, and the genitalia are sometimes pigmented.

*A. lusitanicus*, from egg to adult, is externally similar to forms of *ater* or *rufus*, although external distinctions usually apply to local populations. The juvenile *lusitanicus* is usually strongly banded, and has distinctly closer and more numerous dorsal tubercles than *flagellus*. In the sub-adult and adult from some sites, the sole often becomes nearly uniformly black, but it can also be pale, and, like the whole body, it may be sprinkled, lightly or heavily, with yellow or orange. Internally, *lusitanicus* is distinguished from British *rufus* and *ater* at all stages by its elongate ligula sac, or oviducal bulge, and from *flagellus* by its more fleshy ligula, which is typically long and boat-shaped in contraction (Fig. 3G).

#### CLASSIFICATION OF THE SPECIES OF *ARION*

The significance of egg structure has not been generally recognised, but the British species of *Arion* produce three obviously distinct types of egg, and these provide the simplest and surest means of identifying three major subdivisions in the genus, which are also associated with the three main types of spermatophore. With the subgeneric names in common use, the three groups are:

- (1) Eggs robust and chalky, often large; spermatophores elongate, tapering, with a single longitudinal ridge: *Arion* s.s. and *Mesarion*.
- (2) Eggs thinly coated, soft and sticky, small; spermatophores truncated and more or less hooked posteriorly: *Kobeltia*, including *Microarion*.
- (3) Eggs with a tough flexible integument; spermatophores elongate, polygonal, with fine longitudinal ridges: *Carinarion*.

Only the first of these groups is under scrutiny here. The separation of the subgenera was called into question by Quick's confusion of *A. flagellus* with *A. lusitanicus*, and this problem may be resolved by retaining *lusitanicus* in *Arion* s.s., and placing *flagellus* in *Mesarion*, in which only its coarse tubercles, and perhaps its colour range, appear to be atypical.

#### NOMENCLATURE

##### *A. lusitanicus*

The *A. ater* complex has sometimes been regarded as a single species, because of the individual variation and developmental changes which so often prevent the clear separation of taxa by either the external features or the gross genital anatomy. For the same reason, specific names are generally used in accordance with local or national tradition, without critical evaluation of diagnostic characters, and the nominal species therefore remain poorly understood. In the future, a wider knowledge of the different forms of spermatophore, and the anatomical variation associated with each form, may provide a better foundation for the taxonomy of the complex.

In Britain, different populations of the complex can often be distinguished by external features, but if the populations in a particular locality are not already well known it is unwise to name them without dissection. British *lusitanicus* has often been discovered as a surprise on dissection. While the British *rufus*, described by Quick (1947), is not always clearly separable from *ater*, and may be regarded as a form of that species because of the



spermatophore, the British *lusitanicus*, although externally similar, is quite clearly distinguishable by its spermatophore, as well as the elongate ligula sac which has to accommodate the folded tail of the spermatophore. This British form agrees well with the Portuguese species *A. lusitanicus* Mabille, 1868, as further described and illustrated by Pollonera (1889, 1890) and Simroth (1891). In Simroth's account, *lusitanicus* externally resembles *empiricorum*, and has as many local varieties of colour and size. (*A. empiricorum* Férussac is a nominal species generally synonymised with *A. rufus* (L.), although its spermatophores may not all conform.) *A. lusitanicus* is distinguished by the combination of a true ligula 'of *A. empiricorum*', an oviduct 'of *A. subfuscus*', and a very long epiphallus, producing a long spermatophore. Simroth did not investigate anatomical variation, and further details of the Portuguese forms must be clarified before the typical *lusitanicus* (locus typicus: Serra da Arrabida) can be compared with the British form, the smaller forms of the Azores and Madeira, and others more recently reported in Europe. So far, there appears to be only some slight variation in the proportions of the spermatophore, with general agreement in the character of its denticulation and in the very regular width and curvature of its anterior portion. The spermatophore figured by Simroth (1891, Pl. 6 fig. 2) is exceptionally long and narrow, and is shown with a stream of contents issuing from its tail.

The genitalia and spermatophore of the British *lusitanicus* also agree with some of the figures of the French *A. rufus* of Moquin-Tandon (1855, Pl. 1 figs. 12–16), which are probably the first figures of *lusitanicus*. Mabille (1868), however, first applied the name *lusitanicus* to some of the Portuguese *rufus* described by Morelet (1845), which included some with black lateral bands.

#### *A. flagellus*

Collinge (1893 b, c) reported both *A. lusitanicus* and *A. flagellus* from Ireland, describing *flagellus* as a form intermediate between *lusitanicus* and *subfuscus*. He listed *A. flagellus* as a species of the *ater* group, inhabiting the British Isles and Continent (Collinge 1897). Later, however, when he identified a single 'not quite full grown' English slug as *flagellus*, he considered it to be merely a variety of *A. subfuscus* (Collinge 1904). This specimen, collected by Mr H. Overton in Sutton Park, Sutton Coldfield, has not been traced, and its identification cannot be verified.

Three specimens in the Collinge collection at Cambridge, labelled '*Arion flagellus* Collinge COTYPES Ireland', are evidently the three sent by Mr R. A. Phillips in June 1893, among Irish slugs from unspecified localities: the actual types of *flagellus* and its var. *Phillipsi* being those collected at Schull, Co. Cork, and sent in July 1893 (Collinge 1893 b). Two of the Cambridge specimens show Collinge's dissections, and one of them has the ligula exposed. They can be identified with the Durham slug, distorted to a slightly lesser degree than in Collinge's figures: there is in fact no 'small flagellum' on the oviduct at the attachment of the retractor muscle, but the organs were obviously stretched to give this effect. Although Collinge's description is confused in detail, the identity of his species is not in doubt, and very similar dark brown forms are known in Ireland today. The name *A. flagellus* should therefore be available for the Durham slug.

When Ellis (1974 b) recognised *A. flagellus*, from its original description, as synonymous with *A. lusitanicus*, he was including the Durham slug in this species: he also suggested possible synonymy with '*Arion brevieri* Pollonera (= *A. hibernicus* Brevière)'. The name *A. hibernicus*, which might appear to suit *flagellus*, does not exist, except in error for *A. hibernus* Mabille, 1868. The descriptions of *A. hibernus*, of *A. Brevierei* with its var. *nigra*, and of *A. aggericola* Mabille, 1870, (Mabille 1868, 1870, Brevière 1881, Pollonera, 1887, 1890), have been scrutinised. These indicate the presence in France of rusty-purple, black, and yellowish slugs, which are all possible colour-forms of *flagellus*: but there is no suggestion of coarse tuberculation, and the illustrations in Mabille (1870, Figs. 5–7 *A. aggericola*, and 11–



13 *A. hibernus*) bear much more resemblance to *subfuscus* than to *flagellus*. No types of these species can be found, and the only material which may be original is that of *A. hibernus* in the Bourguignat collection at Geneva. This has been seen: it consists of two small specimens from the type locality 'bois de Meudon, près de Paris'. The smaller has distinct bands, and resembles juvenile *subfuscus*, and the larger, which is probably mature, but now only about 25 mm long, and not dissected, also has traces of banding. The body bands are separated by at least 12 dorsal tubercles. *A. hibernus* was described and illustrated by Mabille (1868, 1870), with no mention or indication of banding, as a rusty-purple slug with a whitish sole, extending to 50 mm in life, and found throughout the winter months in woodlands of the Paris region. The name has been cited as a colour variety of *A. ater* s.l. (Taylor 1905, Quick 1960), or, because of its small size and lack of pigmentation in the sole, *A. hibernus* has been regarded as a juvenile form (Chevallier 1981).

Brevière, like Mabille, examined external features only, and associated different forms with particular habitats and seasons. His *A. hibernus*? was found at Saint-Saulge, only on siliceous soils, and in the winter months. He questioned its identity with Mabille's *hibernus* because it reached a length of 70–75 mm instead of only 50 mm, but its most frequent colour variety was the same rusty purple. He stated that this and two other varieties, one amber and one black, were all completely bandless (Brevière 1881). On receiving from Brevière three examples of the purple form, and one of the black variety, Pollonera (1887) described them as a new species, *A. Brevierei*, distinguished from *hibernus* only by size, and by possessing bands, which were not visible in life, but appeared in alcohol: this phenomenon he had also observed in some forms of *subfuscus*. The genitalia, with a long, cylindrical, oviducal enlargement (Pollonera 1887, Fig. 28), could quite easily belong to a form of *subfuscus*, as was suggested by Chevallier (1972), although Pollonera (1887, 1890) kept *Brevierei* in his *rufus* or *empiricorum* group, rather than the *subfuscus* group. Pollonera (1890) added nothing to Mabille's description of *hibernus*, and its anatomy apparently remained unknown, but he transferred *aggericola* (another yellowish form) from the *subfuscus* group because of its similarity to *Brevierei* in the radula and the genitalia.

It is quite clear that none of these nominal species has been satisfactorily separated from *A. subfuscus*, and *flagellus* cannot be identified with any of them. Neither has *flagellus* yet been found in France.

#### DISTRIBUTION AND ECOLOGY

Problems of identification and nomenclature have obscured and confused many records of *A. flagellus* and *A. lusitanicus*, but both species have undoubtedly undergone expansion in Britain since about 1960. Each sometimes attracts attention as a prolific coloniser of gardens or waste ground, but not together: their origins must be investigated separately.

The 'rediscovery of *Arion lusitanicus*' at Durham, described by Quick (1952), has been shown to be a rediscovery of *A. flagellus*, which had not been recorded with any certainty since Collinge described the original specimens from Schull, Co. Cork, in Ireland, in 1893. Material collected by Mrs S. M. Turk, now deposited in the British Museum (Natural History), accession no, 2342, shows that *flagellus* was present in the Isles of Scilly in 1963, and was widespread, and in some places abundant, in Cornwall in 1963–5 (Turk & Ellis, 1966). Although the first Cornish sites were mostly in or near gardens, it is not necessary to suppose that the species was newly arrived, rather than just newly recognised. It has since been found in many places throughout the British Isles, including some apparently quite remote from human disturbance, where it may have lived unnoticed, or at least unrecognised. Perhaps it survives at low densities in some areas,

retaining, or later acquiring, an ability to multiply rapidly in favourable circumstances. In captivity, a single pair can produce a thousand offspring.

In gardens and farmyards, and on rubbish tips, *flagellus* often appears to have been introduced accidentally with objects on which the slugs were resting, but it seems to spread equally well in relatively undisturbed woodland. In the Croydon district, where slugs have been sampled fairly frequently over 20 years, *flagellus* only appeared for the first time in 1984, but by 1986 it has become abundant throughout two separate areas of woodland, Bramley Bank, Croydon, and Kings Wood, Sanderstead; although it has not been found in other woods, or in any gardens, or on any site that has been invaded by *lusitanicus*.

Dr Quick never found either *flagellus* or *lusitanicus* while he lived at Swansea, but a few examples of *flagellus* were found there in October 1971, both in Clyne Wood, Swansea, and on rough ground near the sea front. It is now known to be widespread in Wales; and its Irish distribution also seems to be mainly western. In eastern Britain, from Sussex to Durham, and in Caithness, records of *flagellus* are more scattered, and it is probably more dependent on the shelter of woods, gardens, or rubbish tips.

Collinge (1987) listed *A. flagellus* as a continental species, but he gave no details, and he may not have had any reliable evidence. Recent attempts to find *flagellus* on the continent have been unsuccessful, and it appears to be confined to the British Isles.

Although *flagellus* may thrive in the same garden as the British *rufus*, *lusitanicus* has only been seen as a local replacement of the other populations of the *ater* complex, among which it can easily remain unrecognised. Collinge probably never had enough material to understand *lusitanicus* well, (see Collinge 1892, 1893 a), although he had European specimens from Pollonera. The only Irish sample which he definitely identified as *lusitanicus* was that collected by Mr H. Burnley Rathborne at Berehaven, Bantry Bay (Collinge, 1893 c), but the two specimens under this label at Cambridge appear on dissection to be rather immature and well banded *ater* s.l., as was reported by Ellis (1968). The external variation of *ater* in Ireland does include some strong and persistent banding, which could have deceived Collinge. His records of *lusitanicus*, therefore, and his account of its colour varieties, may still be doubted. Collinge himself may have had doubts, which could account for the disappearance of the name *lusitanicus* from the British and Irish literature after 1897 for the remaining 50 years of his life. There are a few recent records of *lusitanicus* in Ireland, but there is no proof that the species is native there, or that it has reached Britain from Ireland rather than from the continent.

Although Ellis did not list his records of *lusitanicus* separately from those of *flagellus*, he certainly recognised the two forms, and, under '*Arion lusitanicus*' in the additional species section of the 1969 impression of his 'British Snails', he wrote 'There seem to be two distinct races'. He used to speak of *lusitanicus* as the 'South Devon race', because he had first found it at Alphington, near Exeter, in 1964. In 1965 he found it near the railway station at Penzance, as well as in a sample from a garden at Salisbury. These specimens are preserved in Mrs Turk's collection, BMNH acc. no. 2342. He also recognised it in slugs from West Wickham, Kent, in 1967.

At its only known Scottish site, the Glasgow Necropolis, *lusitanicus* was first identified in 1977, but it could have been established there considerably earlier. In 1986 this still appears to be a stable, isolated population. It probably lacks opportunity to spread in the city of Glasgow or to colonise other sites.

At Hawkhurst, Kent, *lusitanicus* was first seen in October 1974, on rubbish and rotting root vegetables at a roadside, well to the north of the village. This district was not visited again until the dry summer of 1976, when none of the *ater* complex could be found at all, even by night. At the end of October 1981, no *lusitanicus* was found at the original site, but senile and egg-laying individuals were seen by garden walls in the northern part of Hawkhurst, called Highgate.

In 1979 and 1980, *lusitanicus* seemed to be particularly abundant throughout urban and suburban areas of both Exeter and Torquay in Devon, apparently to the complete exclusion of *ater*, which was only seen in Stoke Woods near Exeter, and on sea cliffs at Torquay. Mr Ellis, who was then living at Alphington, observed that all the slugs had suffered badly in the summer droughts of 1975 and 1976, and had only begun to recover in 1978. It seems probable that *lusitanicus* was slightly better able than *ater* to survive and recolonise.

In the Croydon district and the southern fringes of greater London, many slugs were examined in 1967–73, but *lusitanicus* was only found at two sites in West Wickham, Kent, one between a car park and a stream, and the other under an old farm hedge. Many similar sites, and gardens, yielded *ater rufus*, and a few woods *ater ater*. All these were very hard to find in the drier years, and were not seen again until September 1980, when an adult *lusitanicus* was first found in Sanderstead, in a garden where the complex had never been seen before. Investigations the following spring found very numerous juveniles in gardens, and more especially along the old footpath, now between gardens, which once led to Old Fox Farm, Sanderstead. In May 1981, juvenile *lusitanicus* swarmed over damp herbage beside this path, readily dropping off onto anybody brushing past. Suburban foxes make much use of this path, and it is likely that they sometimes carry slugs on their fur when they travel. A slug has occasionally been found accidentally on the tail of a domestic cat, and other animals could also carry slugs, but foxes probably offer the best means of transport between habitats for *lusitanicus* in urban areas. Increases in urban foxes may have had an important influence on the distribution of *lusitanicus* in Britain. The Sanderstead footpath is some 6 km from the sites at West Wickham, separated by much open ground and gardens frequented by foxes.

Since 1981, *lusitanicus* has remained well established in parts of lower Sanderstead and South Croydon, but has not appeared on sites already occupied by *ater* or *rufus*. The species seem to flourish equally, but on separate territories, within boundaries which only become apparent in wet seasons when the slugs are plentiful and emerge on paths and roads.

The behaviour of *lusitanicus* in the garden was first observed in 1981, when the juveniles became conspicuous in April, and grew rapidly to maturity at a length of 10 to 12 cm in July. They were almost as abundant in the garden as on the nearby public footpath, and they appeared regularly at nightfall, especially on the compost heap and on a lawn. They were feeding mainly on vegetable debris, such as fallen petals and mown grass. On the lawn, they selected the grass inflorescence buds, and they would also find and devour any snail that had been accidentally trodden underfoot. From July onwards, a few individuals began to eat some garden plants and seedlings, usually consuming a tender plant completely, before moving on to another. Such individuals, when caught in the act, were removed, and the garden suffered very little additional slug damage attributable to this additional species.

Like *ater*, *lusitanicus* appears to have no effective enemy. The slugs seem to be unattractive to predators, although domestic ducks will seek them out and gobble them up, as one Sanderstead resident has found. The mating slugs do not seek any seclusion, and the few which remain abroad after daybreak do not always make straight for cover. One sub-adult travelled in quite warm sunshine for nearly an hour, on a May morning, across a dew-covered lawn, giving an impression of purposeful homing, or trail-following, before it disappeared quickly into a hole which was no more visible than an earthworm burrow.

The bodies of any *lusitanicus* dying prematurely are likely to be eaten by other *lusitanicus* before any other scavengers. After a wet night at Torquay, numerous groups of mature *lusitanicus*, both living and dying, eating and being eaten, were gathered round the remains of crushed snails in the tracks of traffic on the roads.

The reproductive capacity of *lusitanicus* seems to be very unstable. Whole clusters of infertile eggs are often found, as well as mixed clusters. Sometimes the slugs fail to lay, and become gradually asphyxiated by the pressure of the eggs which accumulate as shown in Fig. 3K. Failure to mate could be a problem, although copulation is not always necessary. An



isolated captive from Exeter produced 9 normal eggs, and 6 of them hatched. It is not at all clear why *lusitanicus* has usually failed to reproduce in captivity, or how its increase is limited in Britain.

In spite of the high densities observed in some of its urban and suburban populations, *lusitanicus* has not been reported as a major pest in Britain. It probably does not surpass the British *rufus* in either the frequency of its attacks, or the severity of their damage to crops. An accurate assessment cannot be made however until more gardeners and farmers can be persuaded to provide specimens for identification. A very different situation is reported in Austria, and other countries, where *lusitanicus* is now regarded as a serious pest, and an alien which may be entirely replacing any native form of the *ater* complex. Reischütz (1984 a, b) describes terrible damage to fields and pastures in Tirol and Vorarlberg (Austria), where the pest spread rapidly from gardens to farms in 1982 and 1983, and acquired the new popular name 'Kapuzinerschnecke'. The relation of this form to the British *lusitanicus*, or to the Portuguese *lusitanicus*, is not clear, and further details will have to be studied.

The story of *A. lusitanicus* in Britain must be seen as only part of the story of a remarkable, but poorly understood, species. Further investigations are needed in other countries, to clarify the taxonomic confusion of the *A. ater* complex and *Mesarion*, and the movements of their invasive forms.

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# NEW OBSERVATIONS ON *HELICELLA STIPARUM* (ROSSMÄSSLER, 1854) (GASTROPODA, PULMONATA, HELICIDAE)

M. T. APARICIO<sup>1</sup> AND M. A. RAMOS<sup>1</sup>

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**Abstract:** A population of *Helicella stiparum* (Rossmässler, 1854) from the surroundings of the city of Almeria (Spain) is studied anatomically and conchologically. In comparison with other ten Spanish species of the subgenus *Helicella*, *H. stiparum* differs in the presence of a free vaginal neck, the smaller dimensions of the dart sacs relative to the size of the shell and genitalia, and in the shape and the inner structure of the dart sacs complex. The eastern species, *Helicella obvia*, *Helicella spiruloides* and *Helicella pappi*, show female anatomical similarities. *H. stiparum* shares with them some of these characters but differs from these species in the thinness of the vaginal neck, the position of the dart sacs relative to the vagina and the shape of the dart sacs complex. The haploid chromosome number ( $n=25$ ) differentiates *H. stiparum* from the rest of the genus *Helicella*. However, the available knowledge concerning most of the *Helicella* species does not allow determination of phylogenetic relationships in this group. New anatomical studies and probably the analysis of new characters are needed to clarify the taxonomy of this genus.

## INTRODUCTION

*Helicella stiparum* was described from the surroundings of the city of Almeria (Spain) by Rossmässler (1854), who pointed out the relationship between this species and *Helicella* (*Helicella*) *itala*, the type species of the subgenus.

Later on, Ortiz de Zárate (1950) studied the genital system of the specimens from the type locality, including the species in the subgenus *typus* of the genus *Helicella*.

The chromosome number of *H. stiparum* ( $n=25$ , Ramos & Aparicio 1985) differs from that of the other *Helicella* (*Helicella*) species already known ( $n=26$ ). This is surprising considering the chromosomic conservatism of the subfamily Helicellinae (Aparicio 1981). This fact, the restricted distribution of the species and some peculiar conchological and ecological characteristics observed, led us to carry out a deep anatomical and conchological study of *H. stiparum* in comparison with other species of the genus *Helicella*.

## MATERIAL AND METHODS

150 specimens of *Helicella stiparum* from Alcores de Punta Entina, Roquetas (Almeria, Spain) (UTM 30S WF 2761) (28–Oct.–82) were collected by hand and fixed in 70% ethanol. Twenty five specimens were dissected and measured using a micrometric ocular and a caliber (0.05 mm.).

The anatomical criterion used is as follows: we consider ‘penis’ the portion from the atrium to the insertion of the penis retractor muscle; ‘epiphallus’ the portion from the penis retractor muscle to the end of the vas deferens; ‘verga’ the structure in the proximal part of the penis when it is open; ‘vaginal neck’ the portion from the insertion of the glandulae mucosae to the insertion of the dart sacs (Polinski 1924, Hesse 1931); ‘free vaginal neck’ the portion from the insertion of the glandulae mucosae to the end of the distal part of the dart

<sup>1</sup> Museo Nacional de Ciencias Naturales (C.S.I.C.) José Gutierrez Abascal, 2. 28006 Madrid (Spain).

sacs; 'dart sacs complex' the structure formed by the two dart sacs and the vaginal duct attached to them. Proximal and distal parts are referred to the genital pore.

Ten *Helicella* species for which accurate quantitative results are available have been used for comparison:

Species	No specimens	References
<i>H. bierzona</i> Gittenberger & Manga, 1977	11	Manga 1983
<i>H. corderoi</i> Gittenberger & Manga, 1977	12	Manga 1983
<i>H. jamucensis</i> Gittenberger & Manga, 1977	13	Manga 1983
<i>H. madritensis</i> (Rambur, 1868)	11	Manga 1983
<i>H. ordunensis</i> (Kobelt, 1883)	25	Manga 1983
<i>H. zaratei</i> Gittenberger & Manga 1977	13	Manga 1983
<i>H. itala</i> (Linnaeus, 1758)	25	Aparicio 1983
<i>H. orzai</i> Gittenberger & Manga, 1981	3 (g.) 27 (s.)*	Gittenberger & Manga 1981
<i>H. mangae</i> Gittenberger & Raven, 1982	20	Gittenberger & Raven 1982
<i>H. striatitala</i> Prieto, 1985	5 (g.) 48 (s.)*	Prieto 1985

\* g.: genitalia; s.: shell.

Three specimens of *Helicella itala* from Burgo de Osma (Soria) and three ones of *Helicella iberica* (Rambur, 1869) from Las Tiesas Bajas (Valle del Estarrum, Huesca) have been used for dissection.

## RESULTS

The numerical results of *Helicella stiparum* are summarized in Tables 1 (shell) and 2 (genitalia). Plate 30 and Fig. 1 show the qualitative characters of shell and genitalia respectively.

The shell is conically depressed similar to that described by Westerlund (1886) and Locard (1894). All the specimens show in the last whorl a keel along the periphery which is less conspicuous towards the aperture. Apart from the tranverse striae there is a very slight spiral microsculpture more marked below the periphery. The great majority of *H. stiparum* specimens show uniform white coloured shells and only nine specimens, out of 150 collected, have shells with a blurred brown striped pattern.

In 17 specimens the complex formed by the two dart sacs and the vagina shows a heart-like form, that is, the distal part is wider than the proximal part. When the structure is opened longitudinally the vaginal duct located along the lower part can be observed (Fig. 2). This duct opens towards the genital pore before the proximal ends of the dart sacs. It has slight and v-shaped foldings (with the apex towards the distal part), but lacks transverse ones, so that the ends of the dart sacs remain free under the conjunctive tissue.

However in *H. itala* and *H. iberica* (Fig. 3), the duct shows transverse foldings at the level of the proximal ends of the dart sacs which join them. Therefore, the proximal part of the whole structure may be distinguishable from the rest. This accounts for the quadrangular shape of the dart sacs complex of these species.

In all the *H. stiparum* specimens studied a free vaginal neck that varies in length can be distinguished and measured (Table 2) with the exception of one specimen in which the insertion of the glandulae mucosae occurs just in the upper border of the distal part of the dart sacs. The vaginal neck has the same structure than the vaginal duct within the dart sacs complex.

*H. itala* and *H. iberica* also have a vaginal neck, but without a free part, that is, the insertion of the glandulae mucosae occurs under the distal part of the dart sacs and before its upper border. In these species the structure of the vagina is continuous along its length and similar to that of *H. stiparum*.

TABLE 1  
Shell quantitative results of *Helicella stiparum*  
SB/UW: shell breath/umbilicus width.

	Whorls	Shell breadth (mm.)	Shell height (mm.)	Umbilicus width (mm.)	SB/UW
max	6.5	18.15	12	4.2	4.77
min	5.5	14	8	3	4.15
$\bar{X}$	6.02	15.89	9.89	3.61	4.42
$S^2_{n-1}$	0.09	1.02	1.11	0.08	0.06
n	25	25	25	25	25

TABLE 2.  
Genitalia quantitative results of *Helicella stiparum*

P+E/F: penis plus epiphallus/flagellum. P/F: penis/epiphallus. S/SD: spermatheca/spermathecal duct. P+E/DS: penis plus epiphallus/dart sac.									
	Mucosae glan. (no)	Verga (mm.)	Penis (mm.)	Epiph. (mm.)	Flagel. (mm.)	P+E/F	P/F	Spermat. duct (mm.)	S/SD
max	24	3.7	7.5	10.2	1.7	15.37	6.5	9.1	1.57
min	9	1.6	3	4.7	0.8	6.86	2.36	2.1	0.31
$\bar{X}$	15.2	2.36	4.96	7.53	1.24	10.25	4.09	5.87	0.63
$S^2_{n-1}$	3.73	0.46	1.19	1.15	0.19	1.92	1.19	1.84	0.25
n	25	25	25	25	25	25	25	25	25
								Longest dart-sac (mm.)	P+E/DS
								3.8	5.54
								2.3	3.18
								3.12	4.03
								0.47	0.63
								25	25
									Free vaginal neck
									0.8
									0
									0.32
									0.2
									23



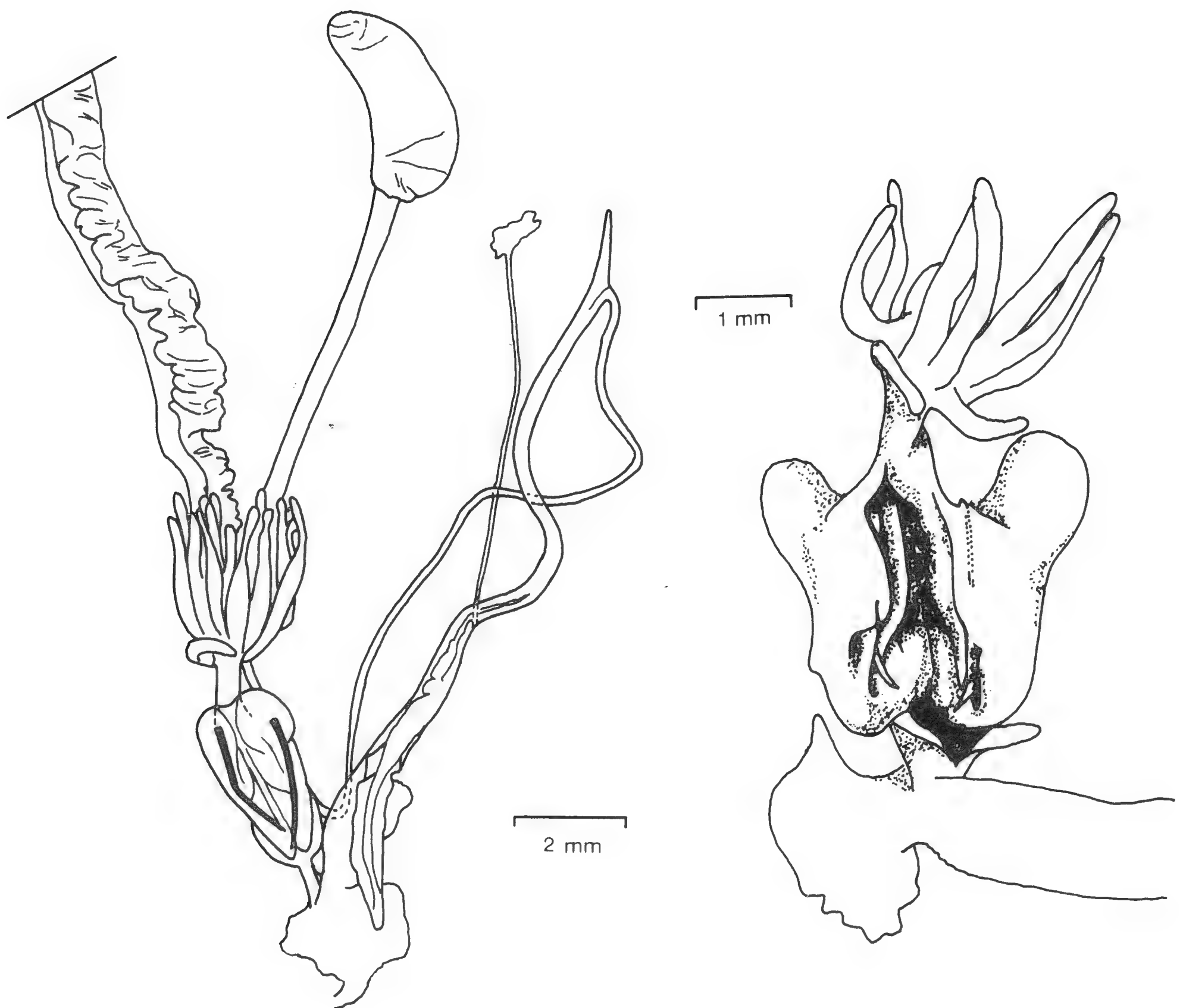


Fig. 1. (left) Genital system of *Helicella stiparum*

Fig. 2. (right) Inner structure of the dart sac complex of *H. stiparum*

The male part of the genital system of *H. stiparum* has a proportionally short flagellum and a verga showing a peculiar shape rounded and slightly lobulated (Fig. 1) that becomes flat at its free end.

In all the 11 *Helicella* species compared, the mean value of the shell breadth, and the mean value of penis plus epiphallus length show a significant positive correlation ( $r=0,93$ ;  $p<0,01$ ) (Fig. 4). This fact suggests that the length of penis plus epiphallus could represent a good estimate of the size of the genitalia in relation to the size of the species.

However, when the mean value of the dart sacs size is plotted against each of the above mentioned characters, *H. stiparum* shows differences with respect to the other ten species. The mean value of shell size is positively correlated with the mean value of the dart sacs size ( $r=0,96$ ;  $p<0,01$ ) when *H. stiparum* is excluded, but the correlation is not significant if it is included ( $r=0,66$ ; n.s.) (Fig. 5a).

In the same way, the mean value of the size of the two genitalia characters, the length of the penis plus epiphallus and the dart sacs size, are positively correlated ( $r=0,89$ ;  $p<0,01$ ) (Fig. 5b) when *H. stiparum* is excluded. The correlation is not significant if it is included ( $r=0,61$ ; n.s.).

The lack of significance in these correlations is due to the small size of the dart sacs of *H.*

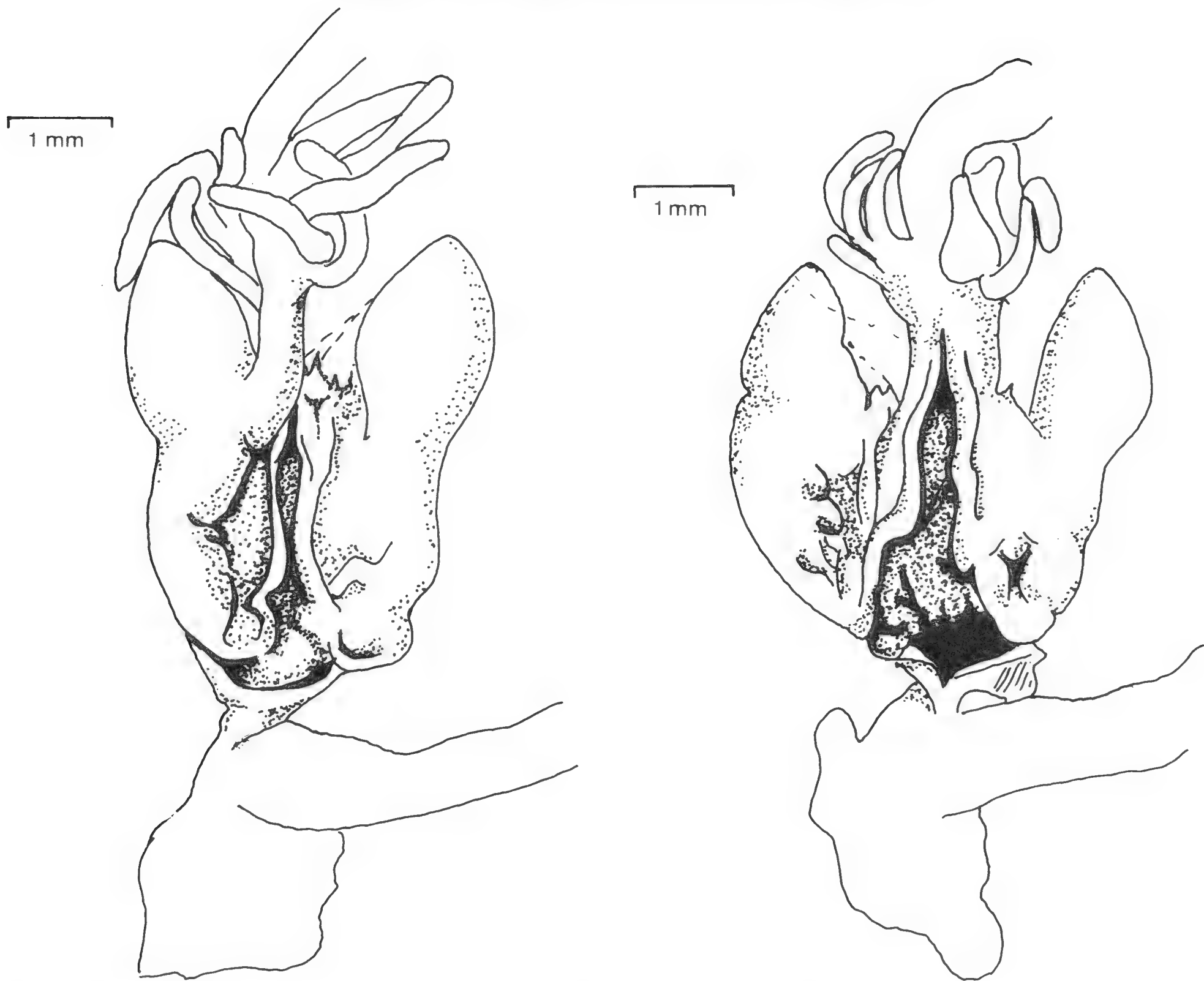


Fig. 3. Inner structure of the dart sac complex of: *Helicella itala* (left); *Helicella iberica* (right).

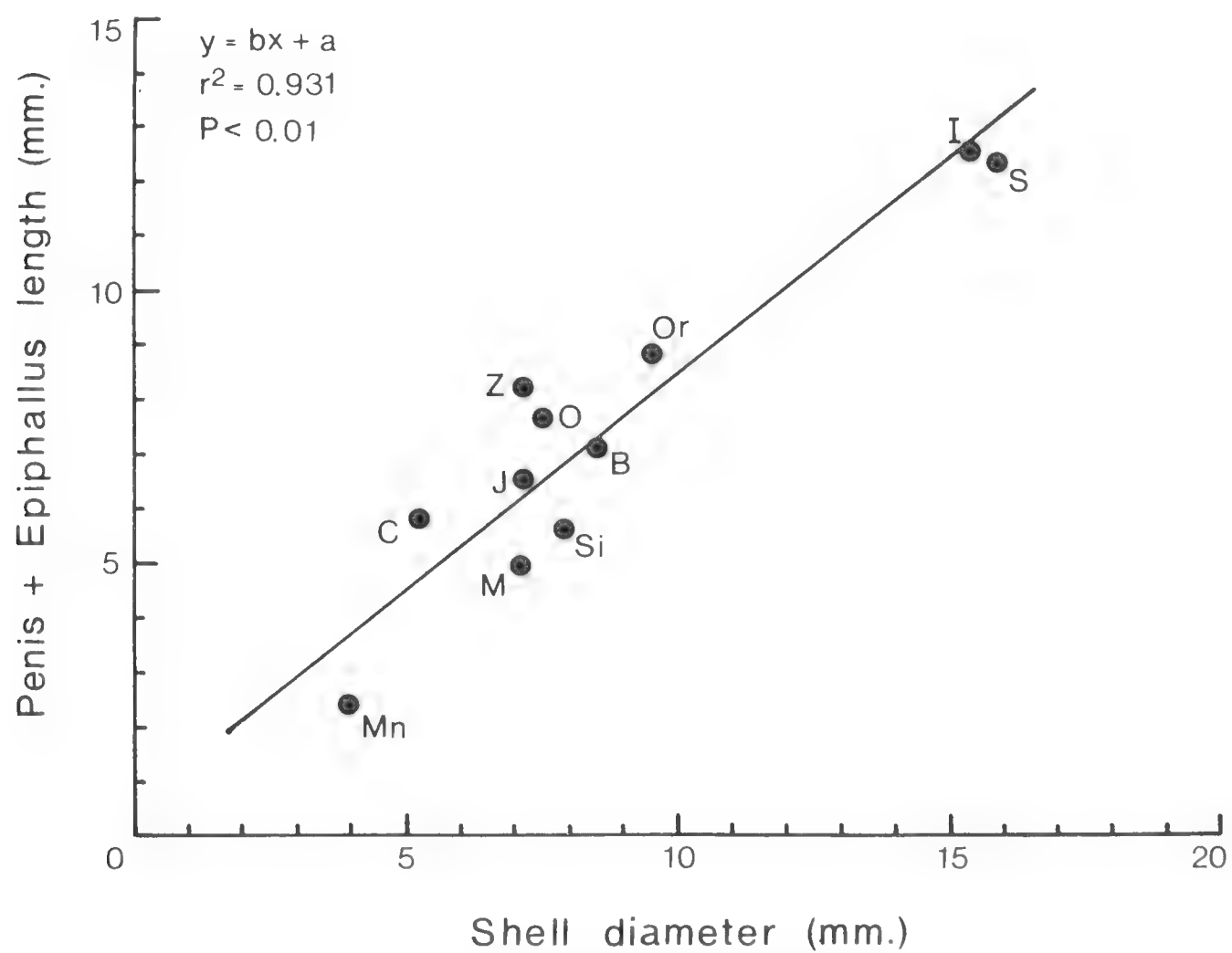


Fig. 4. Correlation coefficient between shell diameter and penis plus epiphallus length of: Mn: *H. mangae*; C: *H. corderoi*; M: *H. madritensis*; J: *H. jamucensis*; Si: *H. striatitala*; B: *H. bierzona*; Z: *H. zaratei*; O: *H. orzai*; Or: *H. ordunensis*; I: *H. itala*; S: *H. stiparum*.

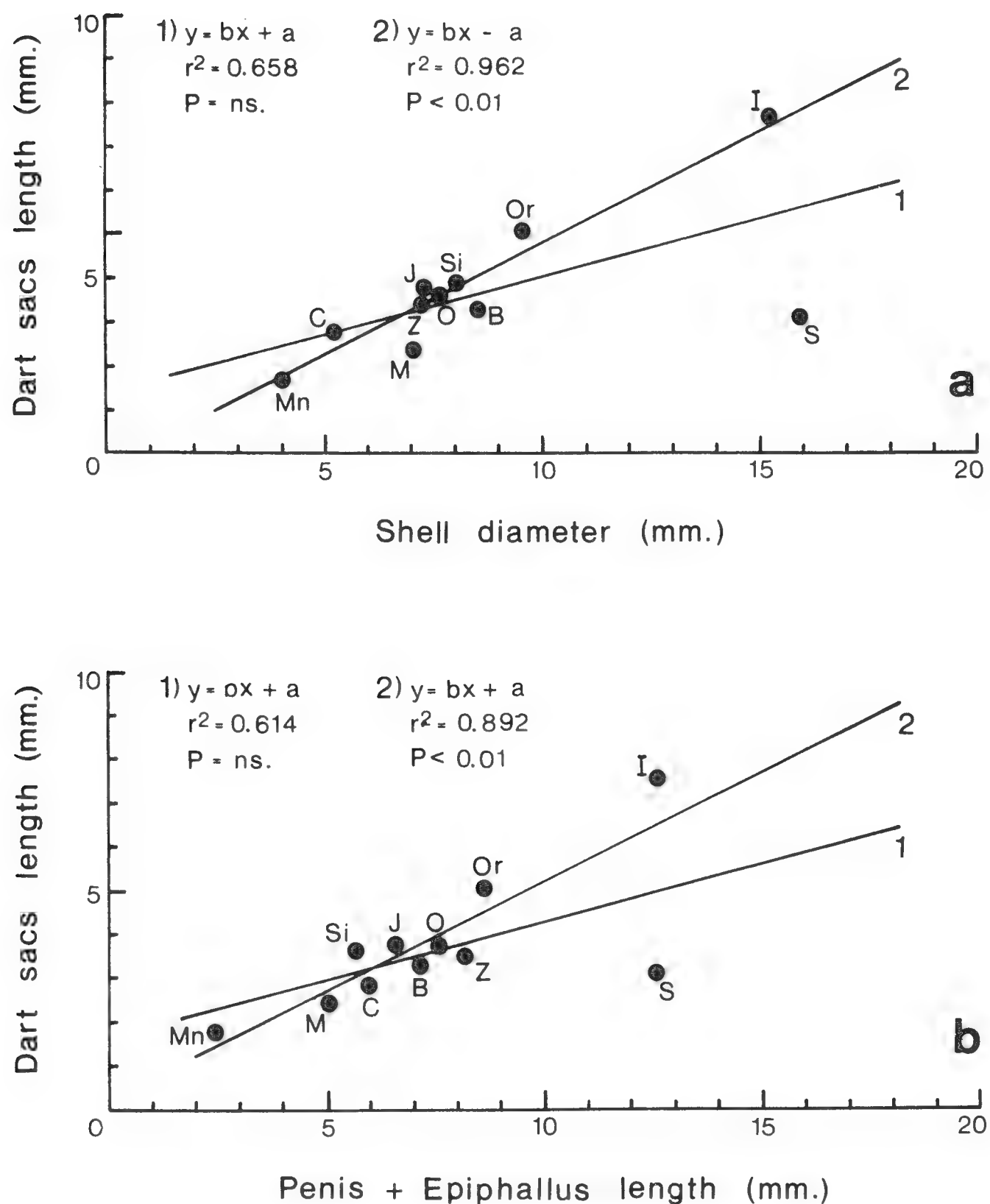


Fig. 5. Correlation coefficients between a: shell diameter and dart sacs length; b: penis plus epiphallus length and dart sacs length. Symbols as in fig. 5. The regression lines marked with 1 include all the species. In regression line 2 *H. stiparum* is excluded.

*stiparum* in relation to its size, allowing the distinction of the vaginal duct at the back of the dart sacs complex.

## DISCUSSION

The genital system of *H. stiparum* shows differences from the other species of the subgenus *Helicella*.

The free vaginal neck observed in *H. stiparum* is not present in all the *Helicella* (*Helicella*) species (except in *H. obvia* and *H. spiruloides*) described till now. In these the insertion of the glandulae mucosae occurs in the vaginal region under the distal part of the dart sacs.

The inner structure of the dart sacs complex of *H. stiparum* also differs from those of the other two *Helicella* (*Helicella*) species that were available for dissection, *H. itala* and *H. iberica*. In *H. stiparum*: a) the portion of the vaginal duct attached to the dart sacs is shorter than in the other species, it does not reach the proximal ends of the dart sacs; b) its aperture does not show transversal foldings; c) the proximal ends of the dart sacs remain free as occurs with the distal ends in all *Helicella* species; d) consequently, the dart sacs complex is heart-like shaped, instead of quadrangularly shaped (longer than wider).

In the ten *Helicella* species studied for comparison the mean value of the dart sacs size increases with average species size. This trend has been also observed in all of the other *Helicella* (*Helicella*) species. However, the available quantitative results for the rest of the species do not allow to estimate mean values and are not included in the analysis. Thus, the dimensions of the dart sacs in relation to the size of *H. stiparum* are significantly smaller than in the case of the other species in this subgenus.

In relation to the subgenus *Xerotracha* Monterosato, it seems that there are no sharp border lines to distinguish it from *Helicella* s. str. Ortiz de Zárate (1950) pointed out the importance of the form and position *in situ* of the darts to characterise the subgenus *Xerotracha* (straight darts that never interlace their points and whose length is short in relation to the length of the dart sacs). However, Gittenberger & Manga (1977, 1981), Gittenberger & Raven (1982), Manga (1983) and Prieto (1985) have mentioned the difficulties involved in the use of these characters, thus, describing new *Helicella* species without subgeneric assignment.

The conchological differential characters of the subgenus *Xerotracha* (small globulous and translucent shell, provided or not with hairs and coloured spots near the suture, and a narrow umbilicus) seem unclear as well, because no defined boundaries can be observed among the *Helicella* species. For example, the breadth of *H. madritensis*, included in the subgenus *Xerotracha* (Ortiz de Zárate, 1950), varies between 6.29–8.71 mm. (Manga 1983), while in other *Helicella* (*Helicella*) species, i.e., *H. itala*, *H. striatitala* and *H. ordunensis* the breadth varies between 7.5–20 mm (Manga 1983), 7.05–9.2 mm. (Prieto 1985) and 6–10 mm. (Manga 1983) respectively.

*H. ordunensis*, which was included by Ortiz de Zárate (1950) in the subgenus *Helicella* (as *H. (H.) alavana*), shows intermediate conchological characters between both subgenera: globose medium size shell, with small umbilicus, opaque, without trace of hair (Prieto 1985).

The monotypic subgenus *Jabalconia* Ortiz de Zárate is characterised by the existence of an appendix in the genital system that clearly distinguish this from the other *Helicella* subgenera.

Schütt (1962) introduced the subgenus *Xerotrachia* for the new species *Helicella pappi* from Greece. No precise anatomical differences between *Xerotrachia* and the other *Helicella* subgenera have been pointed out. Nevertheless, according to the description and drafts of Schütt (1962) the genitalia of *H. pappi* shows: a) two small and wide dart sacs laterally inserted in a wide vagina; b) a vaginal neck that is also enlarged till the insertion of the glandulae mucosae showing a small free portion; c) the dart sacs complex is quadrangularly shaped but differs from *H. itala* (the type species of subgenus *Helicella*) in that it is wider than longer.

In Schütt's opinion the anatomy of *H. pappi* resembles that of *H. obvia* (Menke, 1828) and he suggests the possibility of a genetical relationship between both species. The anatomical characters of *H. obvia* observed in the literature (Paasch 1845, Schubert 1892, Likharev & Rammel'Meier 1952, Grossu 1983) seem to confirm this similarity. The dart sacs of *H. obvia* are thick and inflated with an enlarged vagina protruding between them and showing a short free vaginal neck.

According to Grossu (1983) the Bulgarian species *H. spiruloides* Wagner, 1916 also shows a similar structure but its dart sacs are longer and more slender than in *H. obvia*.

Thus, the female anatomy of these two species seems to be more related to that of *H. pappi* described above, than to the other species of the subgenus *Helicella* s.str.

Schütt (1962) mentions as a conchological characteristic of *H. pappi* the presence of a keeled shell. *H. obvia* and *H. spiruloides* lack this character. However, Frank (1983) indicates that *H. pappi* has forms in which the keel is less prominent or even absent. In fact the shell characters are very variable and seem to be of no relevance among *Helicella* subgenera.



Keeled shells are also found in *H. bierzona* and *H. orzai* whose anatomy belong to the subgenus *Helicella* s.str.

*H. stiparum* shares with the eastern species *H. obvia*, *H. spiruloides* and *H. pappi* the presence of a free vaginal neck, but in *H. stiparum* it is not enlarged. In addition, the vaginal duct of *H. stiparum* is thin and located below and between the dart sacs while in the other three species the vaginal duct is inflated and the dart sacs are laterally inserted in it. The shape of the dart sacs of *H. stiparum* is more similar to the western *Helicella* species than to the wider one found in the three above mentioned species.

On the other hand, the chromosome number of *H. stiparum* ( $n=25$ , Ramos & Aparicio 1985) differs from that of *H. obvia* (Perrot 1938), *H. itala* (Aparicio 1981) and *H. ordunensis* (Ramos & Aparicio 1985) ( $n=26$ ). In spite of the scarce number of species of this genus cytologically analysed, this difference is particularly striking if the chromosomic conservatism in the subfamily Helicellinae is taken into account (Aparicio 1981).

The distribution of *H. stiparum* seems to be restricted to the provinces of Almeria and Granada in Spain (Alonso 1975). The shell is thicker than in the other *Helicella* species. This fact might be considered as an adaptive result of the climatic conditions of the places where it occurs (very high temperatures and high insolation).

The differences and similarities of *H. stiparum* with other *Helicella* species may be mainly due to the fact that we do not have enough data concerning the many *Helicella*-like taxa existing. Therefore at present we do not have suitable criteria to put forward hypothesis about possible relationships among the *Helicella* species.

It seems that the phylogenetic relationships among the *Helicella* species are as problematical as are among the subgenera and may be among genera in the subfamily Helicellinae. A deep revision of these questions probably needs the study of new characters. In this paper we use for the first time the inner anatomy of the dart sacs complex. The study of this structure has provided interesting information in the three species analyzed. However, the estimation of its taxonomical value require the observation of this character in a high number of species.

Thus, we conclude that new anatomical studies are needed to clarify the subgeneric assignment of the species in the genus *Helicella* based on the phylogenetic relationships among the species in that genus.

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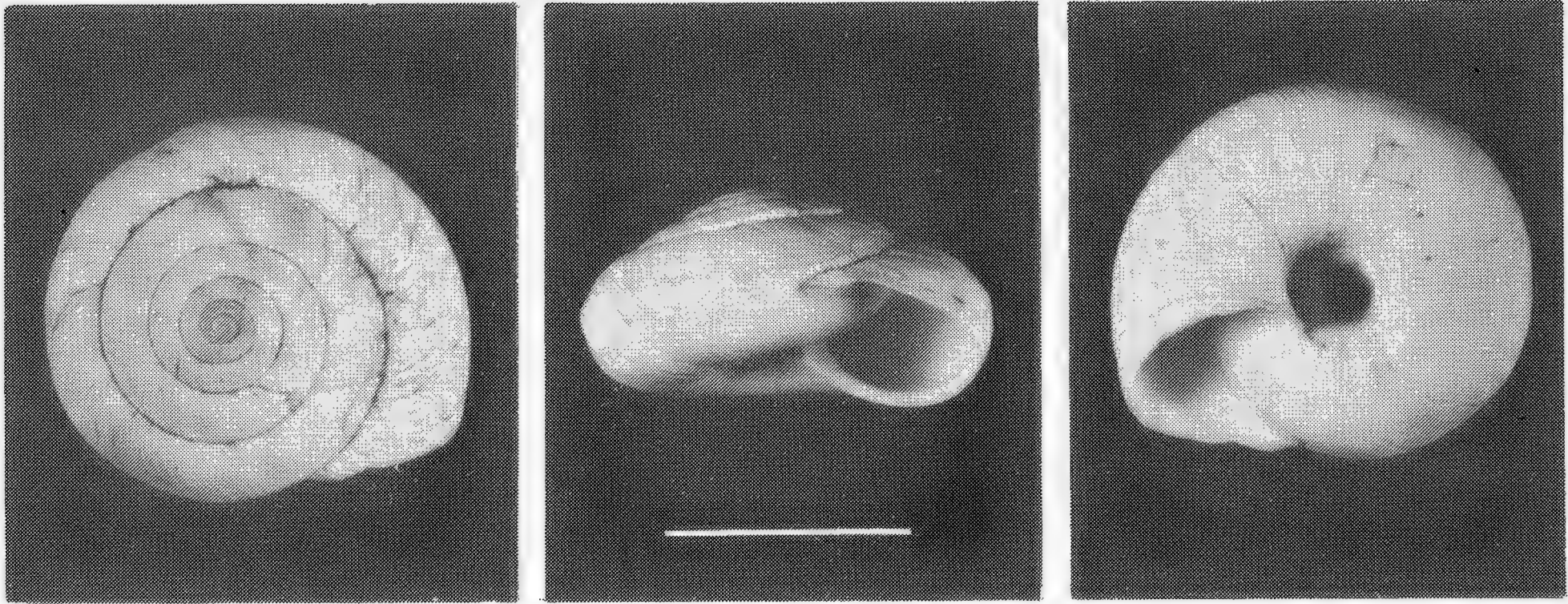


PLATE 30

Shell of *Helicella stiparum*. The bar represents 1 cm.



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# ON THE APHALLY IN THE VERTIGINIDAE (GASTROPODA: PULMONATA: ORTHURETHRA)

BEATA M. POKRYSZKO<sup>1</sup>

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*Abstract:* In 14 of 16 studied species of *Vertigo*, *Truncatellina* and *Columella* among adult and subadult individuals aphyallic ones occur. The aphyally does not appear to result from the penis atrophy following copulation. Combined with small size, short life span, great seasonal fluctuations of population density, eggs laid singly, ability to self-fertilise and copulation of euphallic individuals with aphyallic ones, it appears to be of a high selective value.

## INTRODUCTION

The aphyally in the Vertiginidae was described by Watson (1923) and Steenberg (1925). It was also observed in other orthurethrous taxa – Valloniidae: *Vallonia costata* (Müller), *V. pulchella* (Müller), *V. excentrica* Sterki (Watson 1920, Shileyko 1984), *Acanthinula aculeata* (Müller) (Boycott 1917b, Steenberg 1918, Watson 1920), *Spermodea lamellata* (Jeffreys) (Steenberg 1918), *Zoogenetes harpa* (Say) (Steenberg 1925); Chondrinidae: *Chondrina clienta* (Westerlund) (Steenberg 1925, Shileyko 1984). Outside the Orthurethra it was described in the Zonitidae: *Zonitoides nitidus* (Müller), *Z. excavatus* (Bean) (Watson 1934), *Aegopinella nitens* (Michaud.) (Riedel 1953) and in the Bulinidae – *Bulinus contortus* Michaud. (de Larambergue 1939). Besides, it was noted in some slugs e.g. *Deroceras laeve* (Müller) (Simroth 1885, 1912). In this species, however, the aphyally appears to be of a character entirely different from that in all the above groups.

My recent studies on the reproductive organs of *Vertigo*, *Truncatellina* and *Columella* (Vertiginidae) and observations on the reproductive biology of *Vertigo pusilla* Müller (Pokryszko, in press) have revealed some new facts concerning this phenomenon.

## RESULTS

Aphyallic individuals of *Vertigo*, *Truncatellina* and *Columella* are devoid of male copulatory organs (penis plus genital retractor muscle). The vas deferens (called spermiduct in Fig. 1) in such specimens ends blindly with a slight distension. They do not seem to differ from euphallic individuals in other organs (Fig. 1). Individuals of *Vertigo* and *Truncatellina* attain sexual maturity at the moment of shell completion and the growth does not continue in adult snails. Individuals of *Columella* in all the studied populations become mature at 5 whorls, as indicated by the appearance of their reproductive organs. In specimens just before reaching maturity (ca. 4.0–4.5 whorls in *Vertigo* and *Truncatellina* and slightly less than 5 whorls in *Columella*), i.e. subadult, all the genital organs except the prostatic gland can be distinguished though not yet fully developed. In both the adult and the subadult individuals it can be told if the penis is present. (However, it should be noted that the prostatic gland is visible upon dissection only in *Vertigo*. *Truncatellina* and *Columella* have no distinguishable prostatic gland. It has not been found in subadult *Vertigo*. Even in adult

<sup>1</sup> Museum of Natural History Wrocław University.

individuals it is difficult to notice. Its apparent absence in subadult individuals may be due to its being overlooked or perhaps the organ develops later.)

The aphally appears to be common throughout the Vertiginidae. Aphillic specimens were found to occur in 14 of the 16 studied species (Table 1). Besides, Watson (1923) and Steenberg (1925) described aphillic individuals of *Truncatellina britannica* (Pilsbry) and *T. rivierana* (Benson) respectively.

In 12 of the studied species no hemiphillic specimens were found. In the case of *Vertigo pygmaea* (Draparnaud) and *Columella aspera* Waldén no aphillic individuals occurred in the studied material. In *V. antivertigo* (Draparnaud) and *C. edentula* (Draparnaud), beside aphillic and euphallic specimens, there were also hemiphillic ones. Their male copulatory organs were much smaller than those of the euphallic individuals while the genital retractor muscle was normally developed (Fig. 2). Though in both these species the penis size and shape are somewhat variable among euphallic specimens, it is always easy to tell whether an individual is euphallic or hemiphillic (Fig. 2). It seems that neither between the hemiphillic and euphallic, nor between the hemiphillic and the aphillic condition are there any intermediate stages.

The number of euphallic and aphillic individuals, adult and subadult found in the studied populations is presented in tables 2–4. Populations of which only single specimens were available have been omitted. In *V. pygmaea* and *C. aspera* all the studied adult specimens were euphallic and all the subadult had a penis. In ten species in which both euphallic and aphillic adults occurred, subadult individuals had male organs or were devoid of them. In such species both euphallic and aphillic specimens were found in all populations except those of which only few specimens were available. In four species (Table 3: 5–8) only adult individuals were available for dissection.

The material of most species was too scarce to allow any conclusions concerning interpopulation and interspecific differences in the proportion of both (and in two species three) forms. In two species, however, the material was sufficient to permit at least a preliminary comparison of the frequency of aphillic, euphallic and hemiphillic specimens. The results are presented in Figs. 3 and 4. Two populations of *V. antivertigo*, both sampled in August, differ significantly in the percentage of the three forms (Fig. 3). The difference between two of the four populations of *V. pusilla* Müller (Figs. 4b, c) is also statistically significant. In all the populations shown in Fig. 4 the percentage of aphillic forms is high in spite of the fact that they were sampled at different seasons. However, the difference between populations b and c (Fig. 4) sampled in August and November respectively could be attributed to some seasonal changes. The population from Wojcieszów (Kaczawskie Mts., West Sudetes, Poland) was sampled twice. The percentage of aphillic individuals on June 1st does not differ significantly from that on September 30th (Fig. 5).

Subadult individuals of all the studied species were too few to enable a statistical analysis. The number of aphillic subadult specimens in four populations of *V. pusilla* (Table 3) strongly indicates that in this species subadult specimens having a penis are as rare as euphallic adults.

## DISCUSSION

Possible physiological and/or genetic reasons for the aphillic conditions are unknown. Shileyko (1984) suggests that the aphally in some Orthurethra e.g. *Vallonia* may result from an atrophy of the male copulatory organs following copulation. In the *Vallonia* studied by Shileyko euphallic individuals were found only exceptionally. He found no hemiphillic specimens that could represent intermediate stages of the atrophy process. This fact has led him to make an additional assumption: the penis atrophy is so rapid that its successive

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TABLE 1

Occurrence of euphallic, aphallic and hemiphallic individuals in the studied species.

Species	Euphallic	Aphallic	Hemiphallic
<i>V. antivertigo</i> (Draparnaud)	X	X	X
<i>V. pusilla</i> (Müller)	X	X	
<i>V. substriata</i> (Jeffreys)	X	X	
<i>V. pygmaea</i> (Draparnaud)	X		
<i>V. moulinsiana</i> (Dupuy)	X	X	
<i>V. alpestris</i> Alder	X	X	
<i>V. arctica</i> (Wallenberg)	X	X	
<i>V. ronnebyensis</i> (Westerlund)	X	X	
<i>V. genesii</i> (Gredler)	X	X	
<i>V. geyeri</i> (Lindholm)	X	X	
<i>V. angustior</i> Jeffreys	X	X	
<i>T. costulata</i> (Nilsson)	X	X	
<i>T. cylindrica</i> (Férussac)	X	X	
<i>C. endentula</i> (Draparnaud)	X	X	X
<i>C. aspera</i> Waldén	X		
<i>C. columella</i> (Martens)	X	X	

TABLE 2

Results of dissection of adult and subadult individuals of *Vertigo*: (1) *V. pygmaea*, (2) *C. aspera*

Locality <sup>1</sup>	Date	Adult		Subadult	
		Euphal.	Aphal.	Euphal.	Aphal.
1. Wiżajny nr. Suwałki	21 Aug. 1981	5	0	7	0
Stary Folwark nr. Suwałki	21 Aug. 1981	15	0	4	0
Guzy nr. Suwałki	24 Aug. 1981	6	0	2	0
Sianowo nr. Kartuzy	4 July 1982	—	—	5	0
Lubniewice nr. Gorzów Wlkp.	7 July 1984	5	0	1	0
Łagów nr. Zielona Góra	13 Sept. 1968	3	0	—	—
Podlesice nr. Zawiercie	7 July 1980	2	0	6	0
Romanowo nr. Kłodzko	19 Sept. 1984	1	0	1	0
Wojcieszów nr. Jelenia Góra	14 Sept. 1985	1	0	1	0
Jerzmanice nr. Złotoryja	7 June 1984	2	0	—	—
between Niżnie Sromowce and Wyżnie Sromowce nr. Nowy Targ	17 Sept. 1968	9	0	1	0
Ciecina nr. Żywiec	16 May 1985	3	0	4	0
2. Lubniewice nr. Gorzów Wlkp.	7 July 1984	9	0	6	0
Lubniewice nr. Gorzów Wlkp.	1 Aug. 1985	21	0	7	0
Żubrów nr. Gorzów Wlkp.	1 Aug. 1985	7	0	2	0
Lake Krzywe nr. Gorzów Wlkp.	8 July 1984	6	0	5	0
Łysica, Świetokrzyskie Mts.	21 May 1982	3	0	—	—

<sup>1</sup> All the localities listed in tables 2–4 are in Poland if not indicated otherwise.

TABLE 3

Results of dissection of adult and subadult individuals of *Vertigo*, *Truncatellina* and *Columella*.

(1) *V. pusilla*, (2) *V. substriata*, (3) *V. moulinsiana*, (4) *V. alpestris*, (5) *V. ronnebyensis*, (6) *V. arctica*, (7) *V. genesii*,  
(8) *V. geyeri*, (9) *V. angustior*, (10) *T. costulata*, (11) *T. cylindrica*, (12) *C. columella*

Locality	Date	Adult		Subadult	
		Euphal.	Aphal.	Euphal.	Aphal.
1. Stary Folwark nr. Suwałki	21 Aug. 1981	4	4	—	—
Bakałarzewo nr. Suwałki	23 Aug. 1981	11	31	—	—
Lake Otomińskie nr. Kartuzy	30 June 1982	1	2	—	—
Cisowy Jar nr. Suwałki	24 Aug. 1981	4	7	—	—
Ruciane nr. Olsztyn	1 Oct. 1985	7	27	1	9
Anin nr. Warsaw	13 Nov. 1961	4	38	1	10



Locality	Date	Adult		Subadult	
		Euphal.	Aphal.	Euphal.	Aphal.
Łysica, Świątokrzyskie Mts.	25 May 1982	2	7	—	—
Św. Krzyż, Świątokrzyskie Mts.	26 May 1982	1	1	—	—
Wojcieszów nr. Jelenia Góra	1 June 1981	11	64	3	17
Wojcieszów nr. Jelenia Góra	30 Sept. 1981	10	65	2	14
Czorsztyn, Pieniny Mts.	9 Aug. 1980	1	9	—	—
Sizergh, Cumbria (England)	30 Aug. 1982	1	19	0	1
2. Guzy nr. Suwałki	24 Aug. 1981	2	2	2	1
Ruciane nr. Olsztyn	1 Oct. 1985	4	4	—	—
Anin nr. Warsaw	13 Nov. 1961	6	8	—	—
Krościenko nr. Nowy Targ	9 April 1985	0	3	—	—
Komańcza, Bieszczady Mts.	16 Sept. 1956	1	1	—	—
Kletno nr. Kłodzko	22 July 1982	1	1	—	—
Vogrie House nr. Edinburgh (Scotland)	10 Mar. 1985	4	2	—	—
3. Lubniewice nr. Gorzów Wlkp.	1 Aug. 1985	2	7	—	—
Dziekanów Leśny nr. Warsaw	3 Aug. 1957	21	9	24	8
Chambord nr. Thoury (France)	19 July 1984	2	5	—	—
4. Cisowy Jar nr. Suwałki	24 Aug. 1981	1	2	0	2
Anin nr. Warsaw	13 Feb. 1961	0	2	0	4
Św. Krzyż, Świątokrzyskie Mts.	26 May 1982	4	6	0	1
Św. Krzyż, Świątokrzyskie Mts.	19 June 1973	3	7	0	2
Łysica, Świątokrzyskie Mts.	19 June 1970	4	14	2	9
Czorsztyn, Pieniny Mts.	9 Aug. 1980	1	2	—	—
Dolina Olczyńska, Tatra Mts.	8 Aug. 1984	6	16	2	3
Mały Giewont, Tatra Mts.	9 Aug. 1984	2	4	1	0
Giewont, Tatra Mts.	21 Aug. 1985	13	23	2	6
Przełęcz Małotańska, Tatra Mts.	9 Aug. 1984	2	4	—	—
Przełęcz Tomanowa, Tatra Mts.	19 Aug. 1985	2	2	0	1
Twardy Upłaz, Tatra Mts.	25 Aug. 1985	1	3	2	6
Żar, Tatra Mts.	9 Aug. 1957	1	1	1	1
Coniston, Cumbria (England)	23 Mar. 1985	3	6	—	—
5. Ruciane nr. Olsztyn	1 Oct. 1985	2	3	—	—
6. Twardy Upłaz, Tatra Mts.	26 Aug. 1985	3	6	—	—
7. Tarn Moor, Cumbria (England)	2 Dec. 1984	2	4	—	—
8. Widdy Bank Fell, Upper Teesdale (England)	2 Dec. 1984	5	2	—	—
9. Wigry nr. Suwałki	21 Aug. 1981	1	0	—	—
Nowe Budy nr. Warsaw	1955	0	1	1	0
Romanowo nr. Kłodzko	25 July 1982	8	4	0	1
Gait Burrows nr. Silverdale (England)	26 June 1981	6	5	—	—
10. Osowa Góra nr. Poznań	28 May 1985	4	18	1	7
11. Rebozowo nr. Kartuzy	1 July 1982	0	3	1	5
Checiny nr. Kielce	20 May 1982	0	4	—	—
Podlesice nr. Zawiercie	12 July 1980	2	9	0	2
Czorsztyn, Pieniny Mts.	9 Aug. 1980	0	12	0	1
12. Niżnia Świstówka, Tatra Mts.	14 Aug. 1985	2	1	—	—
Wyżnia Świstówka, Tatra Mts.	14 Aug. 1984	7	3	8	8
Przełęcz Małotańska, Tatra Mts.	9 Aug. 1984	2	1	—	—
Twardy Upłaz, Tatra Mts.	26 Aug. 1985	2	5	6	4
Ciemniak, Tatra Mts.	26 Aug. 1985	3	2	—	—
Krzesanica, Tatra Mts.	26 Aug. 1985	3	2	—	—
Giewont, Tatra Mts.	21 Aug. 1985	1	4	—	—
Kominiarski Wierch, Tatra Mts.	23 Aug. 1985	0	2	—	—
Przełęcz Tomanowa, Tatra Mts.	19 Aug. 1985	2	3	—	—

TABLE 4  
Results of dissection of adult and subadult individuals of *Vertigo* and *Columella*  
(1) *V. antivertigo*, (2) *C. edentula*

Locality	Date	Euphal.	Adult		Hemiphal.	Subadult	
			Aphal.			with penis	with no penis
1. Stary Folwark nr. Suwałki Wigry nr. Suwałki Lubniewice nr. Gorzów Wlkp. Leszczyny nr. Kielce Czarny Las nr. Kielce Świeta Katarzyna nr. Kielce	21 Aug. 1981	11	13		38	13	5
	24 Aug. 1936	6	3		5	5	1
	2 Aug. 1985	11	4		5	7	2
	7 Aug. 1981	23	6		27	11	9
	5 Aug. 1981	3	0		1	1	0
	22 May 1982	2	1		1	—	—
	30 Aug. 1981	3	1		1	2	0
	23 Aug. 1981	10	1		5	5	1
2. Romincka Forest nr. Suwałki Lake Siekierewo nr. Suwałki Lake Otomińskie nr. Kartuzy Ruciane nr. Olsztyn Mielenko nr. Koszalin Spadowiec, Tatra Mts. Dolina Kościeliska, Tatra Mts. Brigsteer Wood nr. Levens, Cumbria (England)	25 June 1982	5	1		3	—	—
	1 Oct. 1985	3	1		1	3	0
	30 Aug. 1985	5	0		0	4	1
	7 Aug. 1984	12	1		4	6	2
	6 Aug. 1984	10	0		2	7	1
	6 April 1985	12	2		5	—	—

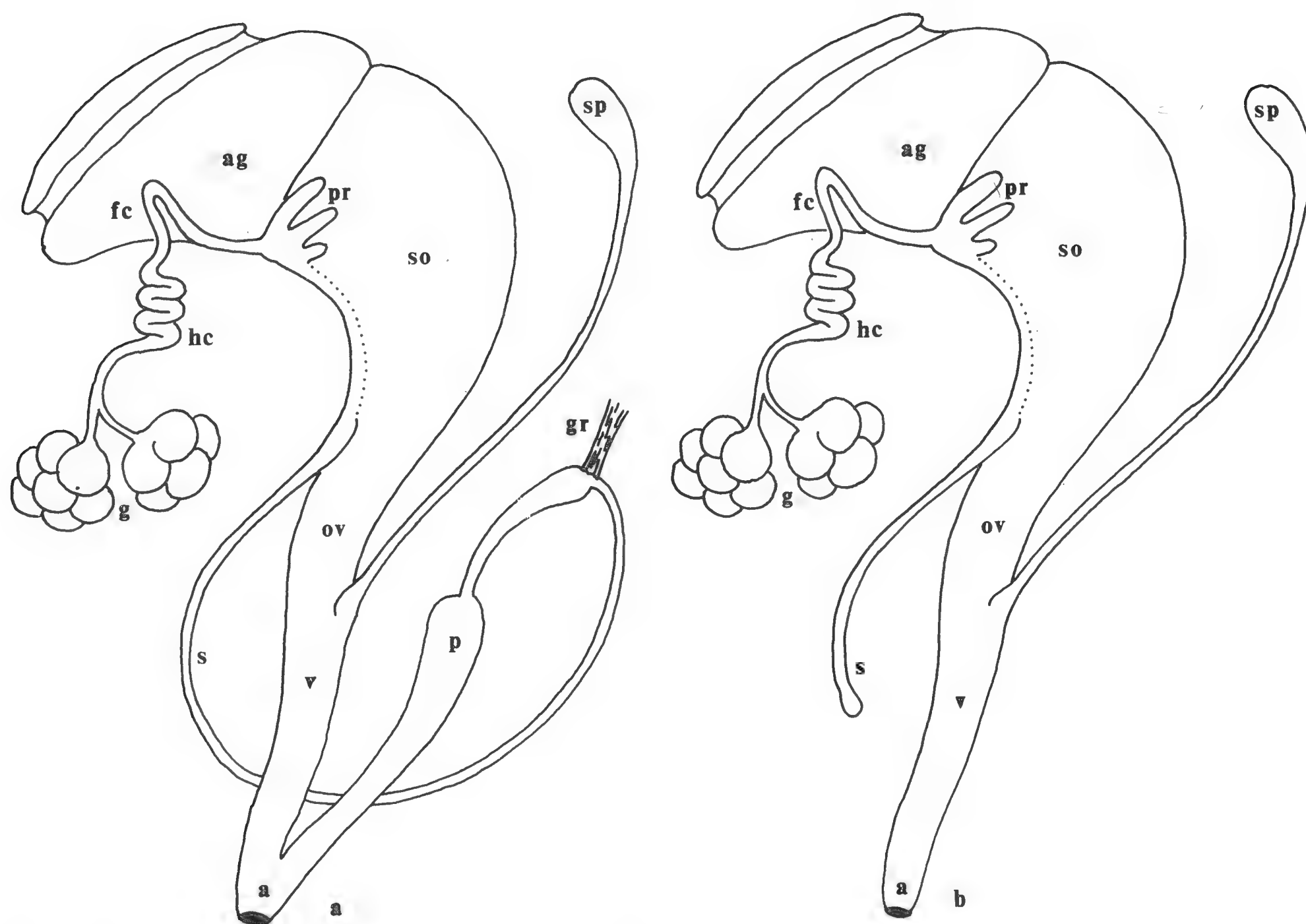


Fig. 1. Reproductive organs of euphallic (a) and aphallic (b) vertiginids.

g – gonad, hc – hermaphrodite canal, fc – fertilisation chamber, ag – albumen gland, pr – prostatic gland, so – spermoviduct, s – spermiduct, sp – spermatheca, ov – free oviduct, v – vagina, p – penis, gr – genital retractor muscle, a – genital atrium.

stages can not be observed (Shileyko 1984, p. 47). He admits, though, that in some taxa e.g. the Chondrinidae, in which aphallic individuals are found along with euphallic ones, the aphally is of different character, but makes no statement pertaining directly to the Vertiginidae.

Some consequences of the 'rapid reduction hypothesis' can be easily predicted.

1. If the male organs underwent reduction following copulation, all the individuals that have not copulated (e.g. subadult) would have a penis. The results presented above show that in most species, beside subadult individuals that have a penis, there are individuals devoid of it. In *V. pygmaea* and *C. aspera* all the adult individuals are euphallic and all the subadult specimens have male organs.

2. If the penis underwent reduction, no matter how rapidly, some stages of the process could be observed especially if sufficient material was studied. I have dissected ca. 1000 adult individuals collected at various seasons and coming from various populations. Hemiphallic individuals have been found in two species only. In those two cases the morphological gap between the euphallic and the hemiphallic condition was quite distinct. Additionally, in both those species, among subadult specimens, there were both individuals which had a penis and ones devoid of it. Thus, it is difficult to interpret the hemiphallic condition in the Vertiginidae as an evidence for the penis reduction. It is more probable that the hemiphallic condition in *V. antivertigo* and *C. edentula* (Drapernaud) results from some functional changes in their male organs. If such a solution is adopted, the following question will arise. Why are there no comparable functional changes in most of the studied species?

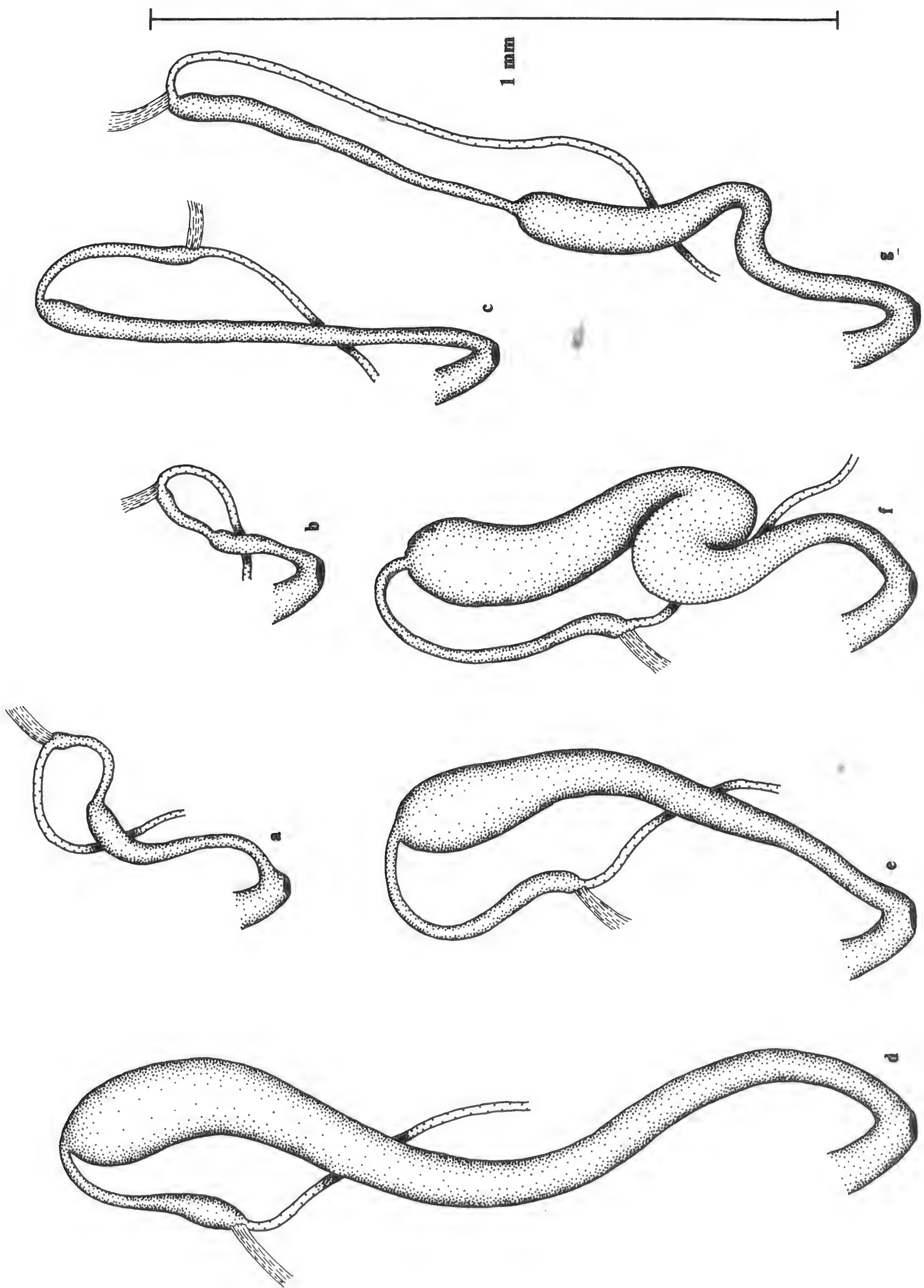


Fig. 2. Penis variation in *V. antiwertigo*. a, b, c – hemiphallic, d, e, f, g – euphallic. Leszczynny nr. Kielce, Poland, 7. Aug. 1981.



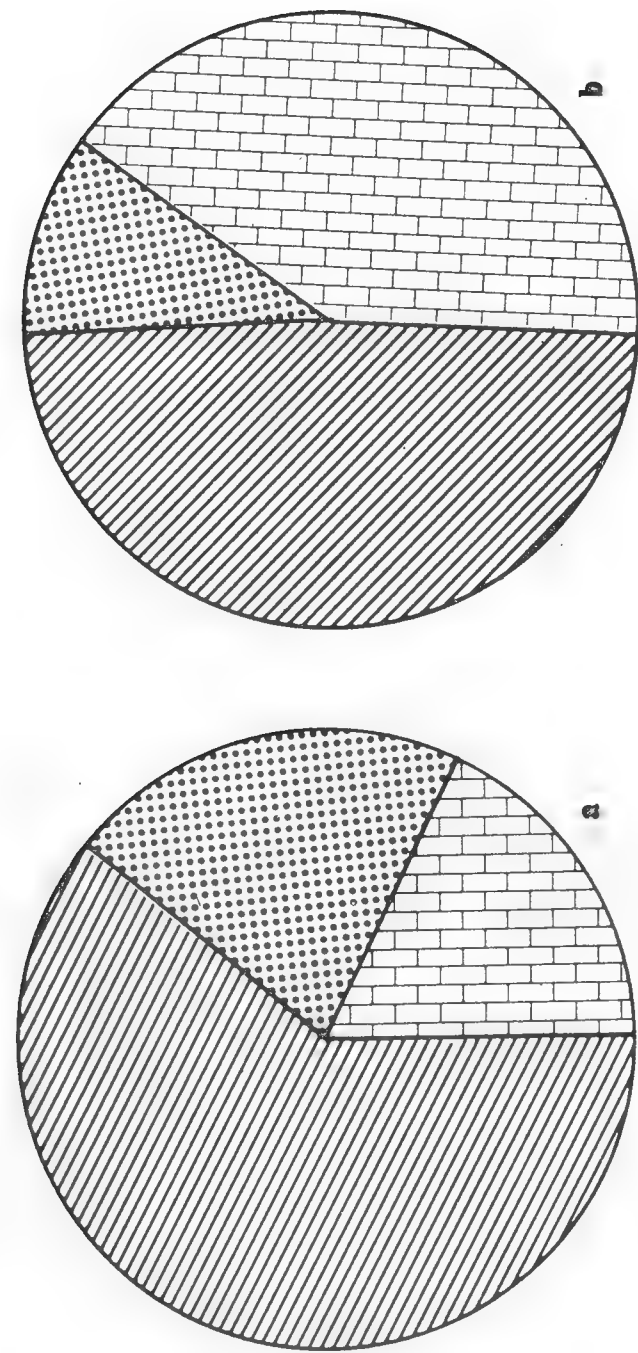


Fig. 3. Proportion of euphallic (bricked), hemiphallic (hatched) and aphallic (dotted) individuals in two populations of *V. antiverigo*. a – Leszczyny nr. Kielce, Poland, 7 Aug. 1981 (56 specimens), b – Stary Folwark nr. Suwałki, Poland, 21 Aug. 1981 (62 specimens).

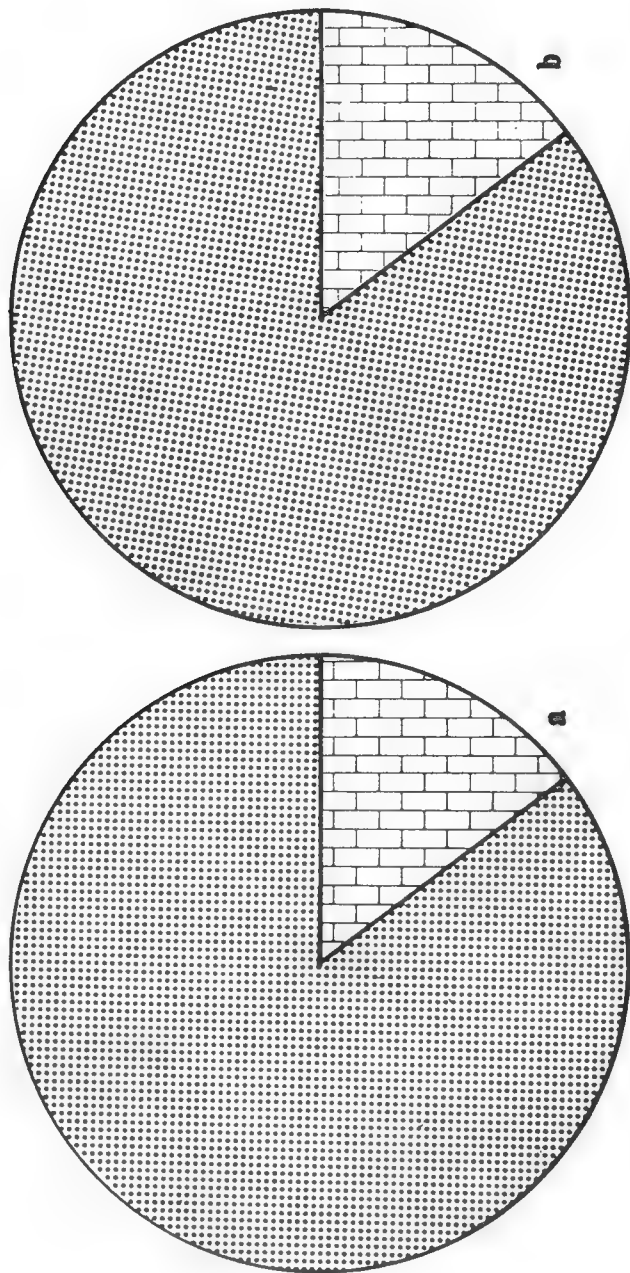


Fig. 5. Proportion of aphallic (dotted) and euphallic (bricked) individuals in two samples from population of *V. pusilla*. Wojcieszów nr. Jelenia Góra, Poland: a – 1 June 1981 (75 specimens), b – 30 Sept. 1981 (75 specimens).

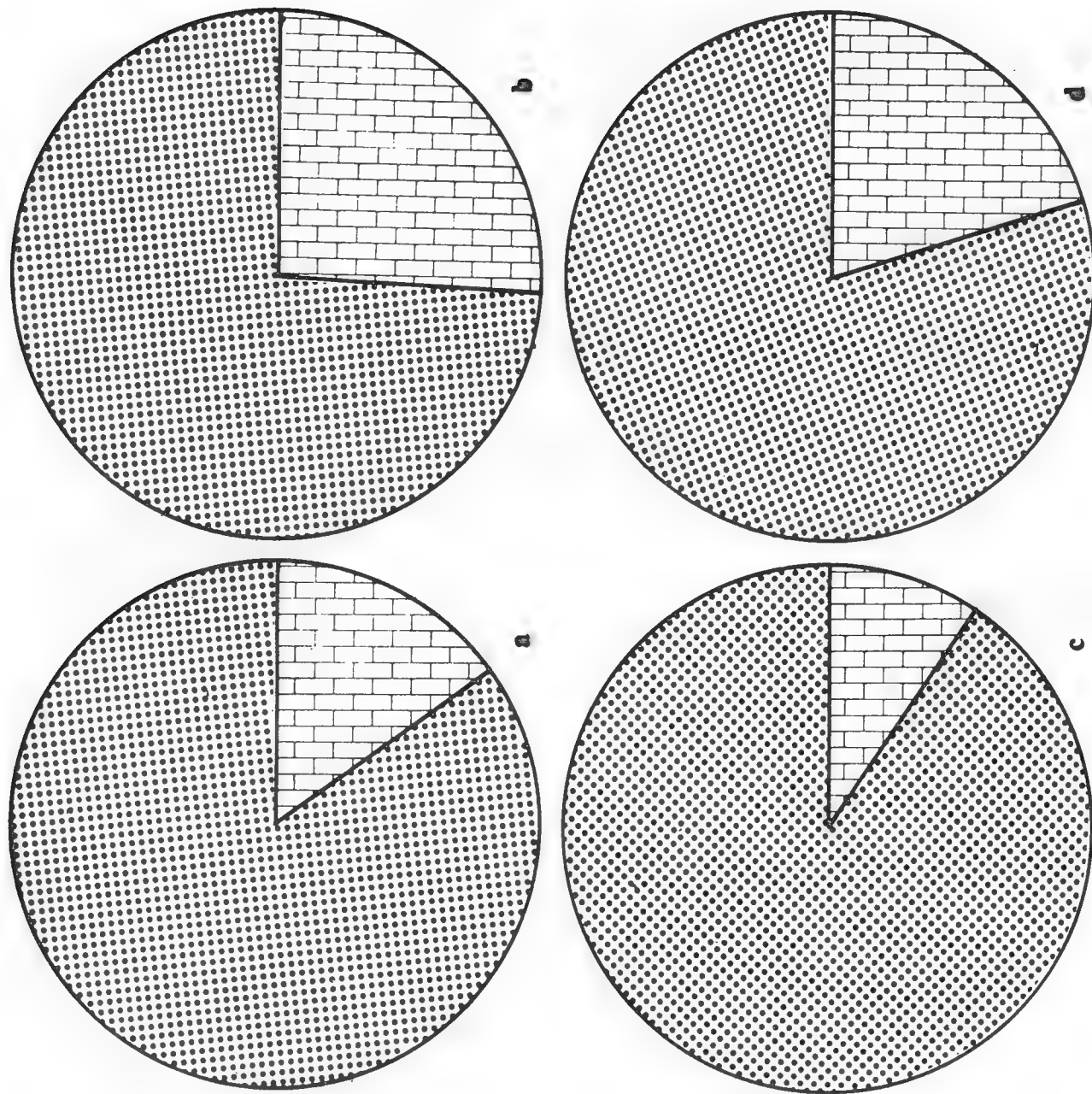


Fig. 4. Proportion of aphallic (dotted) and euphallic (bricked) individuals in four populations of *V. pusilla*. a – Wojcieszów nr. Jelenia Góra, Poland, 1 June 1981 (75 specimens), b – Bakałarzewo nr. Suwałki, Poland, 23 Aug. 1981 (42 specimens), c – Anin nr. Warsaw, Poland, 13 Nov. 1961 (42 specimens), d – Ruciane nr. Olsztyn, Poland, 1 Oct. 1985 (34 specimens).

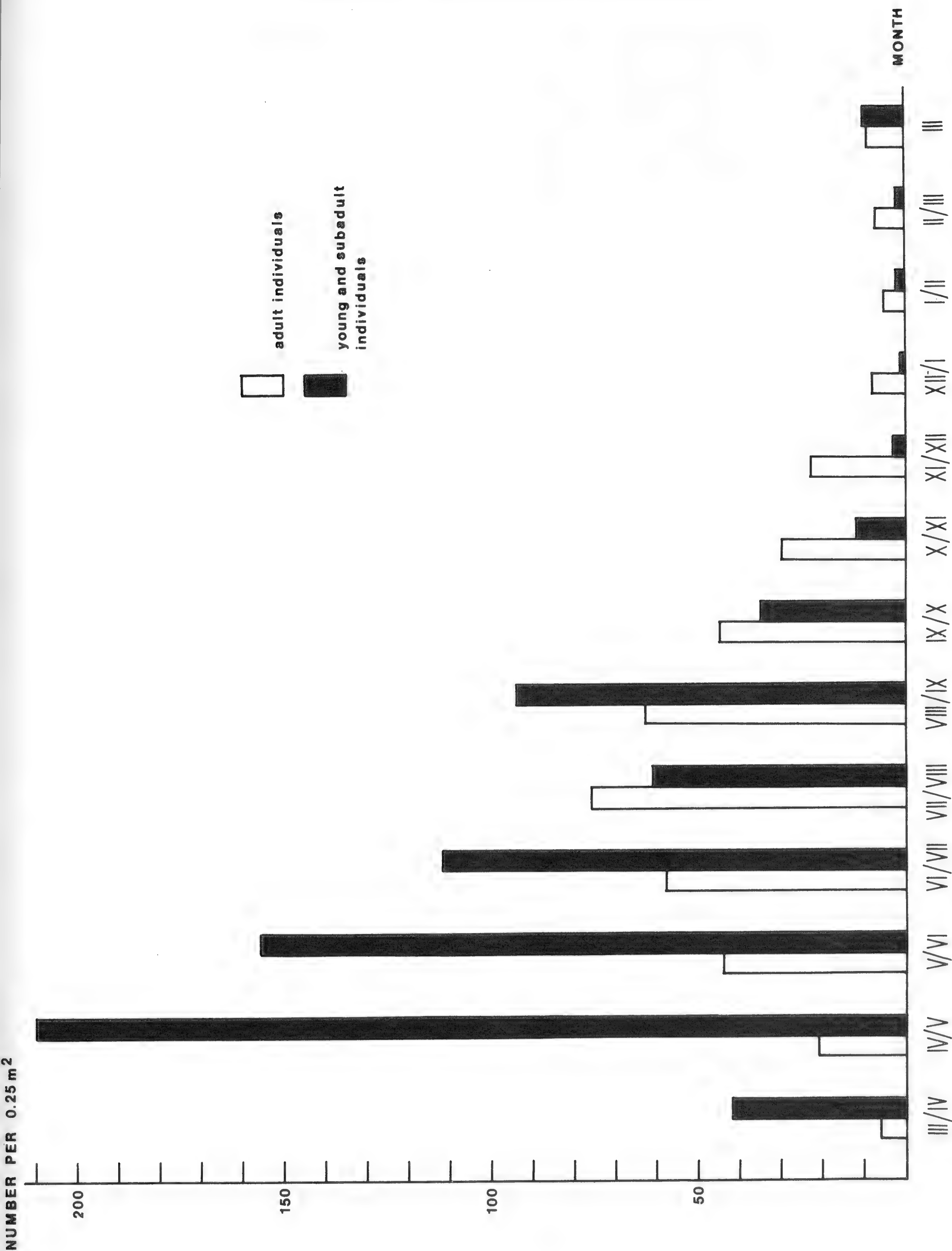


Fig. 6. Population of *V. pusilla* from Wojcieszów nr. Jelenia Góra, Poland. Seasonal changes in density and age structure. Samples were taken at monthly intervals, at the turn of each month, except for the last sample (March 11th), from March 1985 until March 1986.

3. If the euphallic condition changed into the aphyallic one following copulation, the percentage of aphyallic individuals could be expected to show seasonal fluctuations. There are no differences between samples taken at different seasons from the population of *V. pusilla* (Fig. 5). In various populations of this species, sampled at different seasons, despite minor differences, aphyallic individuals are always much more numerous than euphallic ones. Watson (1923) and Steenberg (1925) did not notice any dependence between the season and the percentage of aphyallic individuals.

The results presented in this paper indicate that the individuals of the studied species of *Vertigo*, *Truncatellina* and *Columella* from the beginning of their life either have male copulatory organs or are devoid of them. Of course, this is just one more hypothesis. A final proof can be expected to come from genetic and development studies. Such studies were done on *Bulinus contortus* and it has been found that the aphyally in this species is a genetically transmitted character (de Larambergue 1939). No comparable study has been done on any orthurethrous snail.

The biological significance of the aphyally in the Vertiginidae seems to be at least partly explained. In *V. pusilla*, the only species whose life history has been studied (Pokryszko, in press) euphallic individuals function as 'males', aphyallic – as 'females' during courtship and copulation. Specimens of this species, as well as those of *V. alpestris* Alder and *V. substriata* (Jeffreys), kept in isolation from early development stages, lay viable eggs. *V. pusilla* can reproduce in this way for a few generations, apparently without its reproductive ability being affected. This seems to be its usual method of reproduction since in all the studied populations euphallic individuals are relatively few. The same has been found for *Vallonia pulchella* (Whitney 1937), a species in which euphallic individuals are found only exceptionally.

The selective value of the aphyally, be it a penis reduction after copulation or an hereditary trait, is another problem. A solution of it was first proposed by Boycott (1917a,b) who saw the main reason in poor locomotory abilities of small snails. This would cause difficulties in meeting of potential partners. Under such circumstances the loss of the penis and the ability to self-fertilise would be of advantage. Watson (1923) suggested that with the decrease in size minute forms such as the Vertiginidae had to dispose of some organs e.g. penis. None of these hypotheses can wholly explain the phenomenon. Objections they raise have been summarized by Riedel (1953). This author attributes the main effect to ecological conditions. Though his considerations pertain mainly to the Zonitidae, the aphyally in the Vertiginidae may have at least partly ecological reasons. The density in the studied population of *V. pusilla* shows great seasonal fluctuations (Fig. 6). At the end of winter, just before the reproductive activity begins, adult individuals are relatively few and at the beginning of the breeding season the probability of meeting of two specimens is the lowest. The few individuals that have survived winter are able to reconstruct the population in a few weeks. The spring density peak reaches ca. 1000 specimens per square metre. This would be probably impossible if there were no self-fertilisation. The number of adult individuals is the highest in July/August, and thus the probability of encounters and, in consequence, of copulations is much higher than in the spring. A minor reproductive peak may appear in August/September if the weather is favourable. Individuals of *V. pusilla* (and those of *V. alpestris* and *V. substriata*) lay eggs singly or – rarely – in twos, at intervals of 12 hrs or more. The number of eggs produced per individual lifetime varies widely (5 to more than 30). Generally, this method of reproduction can be called 'single egg many times' as opposed to the method found in many other snails 'many eggs a few times'. The egg-laying in *Vallonia pulchella* is similar (Whitney, 1937). Even if a number of eggs are laid as a result of copulation, it is possible that after the allosperm stored in the spermatheca has been used, self-fertilisation takes place and next eggs are laid instead of waiting for another chance to copulate.



The aphally considered out of the ecological and biological context may be of no advantage. As a part of the life history pattern involving short life span (1–1.5 year in *Vertigo*), small size, large density fluctuations, large eggs laid singly, ability to self-fertilise when no partner is available and euphallic-aphallic copulation whenever possible, it may be of a high selective value. The reproductive biology of *Truncatellina* and *Columella* is obscure, and it is difficult to envisage how these two genera could benefit from the aphallic condition. However, its high selective value seems to be evidenced by the fact that it is so common throughout the Vertiginidae.

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# AN UNDESCRIBED SPECIES OF *ZONITES* FROM THE ISLAND OF SANTORINI, GREECE

ADOLF RIEDEL<sup>1</sup> AND ADRIAN NORRIS<sup>2</sup>

(Accepted for publication, 23rd May 1987)

**Abstract:** *Zonites (Zonites) santoriniensis* is described as a new species from the Island of Santorini, Greece, and the distribution of *Zonites* in the Cycladic Islands is discussed.

## INTRODUCTION

The genus *Zonites* Montfort is known from the following Cycladic Islands; including the most westerly of the Dodecanese (Riedel 1985): Dilos (introduced in the past and now extinct? – see Riedel 1985, p. 45), Naxos, Keros (subfossil only), Donousa (New Record – Mylonas, subfossil only), Amorgos, Kinaros, Astypalaia, Ofidousa, Sifnos (subfossil only), Folegandros (subfossil only), Sikinos (subfossil only) and Anafi. None of the other Cycladic islands investigated by Mylonas (1982) produced records of the genus *Zonites*. However, Mylonas (pers. comm.), expressed the opinion that this genus should be present, (if only in the fossil record), on the island of Santorini (= Thera or Thira). Santorini is situated between the islands of Folegandros and Sikinos to the north-west, and Anafi to the east.

In May 1986 one of the authors (AN) visited the island of Santorini and discovered a number of fossil shells of the genus *Zonites* which subsequently proved to be a new species. This discovery confirms the opinion that *Zonites* should occur on the island as it is situated within the known distribution of the genus in the Cyclades, and has biotopes suitable for *Zonites*.

### ***Zonites (Zonites) santoriniensis* sp. nov.**

**Types Locality:** Base of limestone crag by the footpath from Perissa to Archaia Thira in the south-east part of the Profitis Ilias massif, Santorini, Cyclades, Greece.

**Material:** 19 subfossil shells of various ages, sizes and condition. May 1986, A. Norris leg. The shells were found in a carbonate + humus, soil solidified to form a calcrete, in which they were embedded, and with which they had become encrusted, (see Pl. 31, fig. 1).

**Holotype:** British Museum Natural History, (BMNH 1986–233); paratypes (10) located in the Leeds City Museum (LEEDM–C–10–1986); Institute of Zoology, Polish Academy of Sciences, Warsaw (3) and in A. Norris collection (5).

**Shell:** (Holotype Pl. 31, figs. 2–4), large (diameter to 37.4 mm), very low conical, flattened above and below, with a low but distinctly and regularly convex spire and obtuse apex; spire forming a step only between the last or body whorl and the penultimate whorl in the fully developed shell. Whorls  $5\frac{1}{2}$ –6 (?), increasing slowly and regularly, the body whorl being about 1.8 times as wide as the penultimate; weakly convex (including embryonic whorls) with very shallow sutures; the last  $\frac{1}{2}$ – $1\frac{1}{2}$  whorls of adult shell usually a little more convex with a deeper suture. Distinct suprasutural depression, connected with the formation of a keel, visible at least on the middle whorls. The periphery of the last whorl in adult shell, (in profile), obtuse angular to rounded, in subadult – angled to keeled, in

<sup>1</sup> Institute of Zoology, Polish Academy of Sciences, 00–679 Warszawa, Wilcza 64, Poland.

<sup>2</sup> Leeds City Museum, Municipal Buildings, Leeds LS1 3 AA, West Yorkshire, England.

juvenile – always sharply keeled, the keel or angle being situated in the mid-line of the periphery. Underside of shell convex, umbilicus funnel-shaped, deep and comparatively wide, with all whorls visible. Aperture oval. Upper surface of shell with a distinct spiral granulation (Pl. 31, fig. 8); on the last whorls the granulation is rougher and not as regular as on the earlier, (including embryonic), whorls. Sculpture of the underside much weaker. *Holotype*: major diameter 35.4 mm, minor diameter 29.4 mm, height parallel to the axis 21.2 mm, height by oblique axis 18.8 mm, 5.3/4 whorls (counted by Ehrmann's method; after Kerney and Cameron 5½). (All three specimens larger than the holotype have the initial whorls destroyed).

Shell variable in height and development of the angle or keel on the periphery, especially in subadult specimens. Some, (Pl. 31, fig. 5), resemble *Z. siphnicus* Fuchs and Käufel (Riedel 1985, p. 38, Pl. III figs. 28–32), but differ in possessing a suprasutural depression, stronger granulation of the upper surface and in the sculpture of the embryonic whorls; others (see Pl. 31, fig. 6) resemble *Z. anaphiensis* Riedel and Mylonas, but in the latter species the shell is more flattened below and the keel is lower down the periphery (Riedel and Mylonas 1981, Pl. 1, fig. 1). Fully adult shells of *Z. santoriniensis* are bigger than both *Z. siphnicus* and *Z. anaphiensis*, and differ distinctly from *Z. anaphiensis* in the rounded (not keeled), periphery. Juvenile shells of *Z. santoriniensis* (Fig. 7) differ clearly from young *Z. siphnicus* (see Riedel 1985, Fig. 29), in that they are sharply keeled and not just angular on the periphery.

The identity of the subfossil *Zonites* from Sikinos, mentioned by Riedel (1985, p. 39, Pl. III figs. 33–35) as *Z. siphnicus* ssp.?, may be a form of *Z. siphnicus* or of *Z. santoriniensis*. The known material (2 specimens) is too limited to resolve this problem.

*Remarks*: *Z. santoriniensis* is probably an extinct endemic species, as no recent shells were found during either the intensive malacological field work carried out by Mylonas, or during independent visits to Santorini by the authors in 1986. The extinction of this snail may be a consequence of the eruption of the volcano on Santorini circa 1,500 B.C., which resulted in the island, (including the biotope of *Zonites*), being covered with a thick layer of pumice and volcanic ash. It is remarkable that, with the exception of the subterranean *Lindbergia beroni* Riedel 1984, (from the Zoodochos cave), there are no endemic species among the contemporary malacofauna of Santorini, the number of endemics is especially high on other islands in the southern Cyclades (e.g. Anafi, see Mylonas 1982 and 1984, Fig. 4). The majority of the old malacofauna of Santorini must have been destroyed by the volcanic explosion, and over the last 3,500 years the island has been colonized by the more expansive species from adjacent islands and by those species particularly associated with the activities of man, (anthropochorous species).

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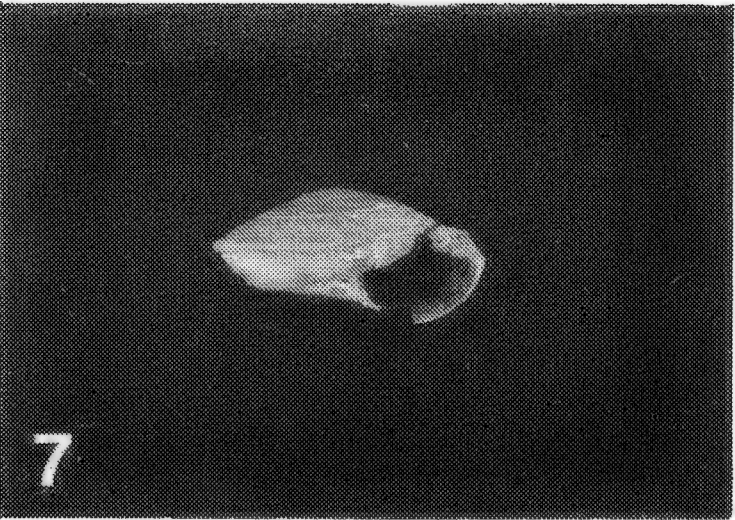
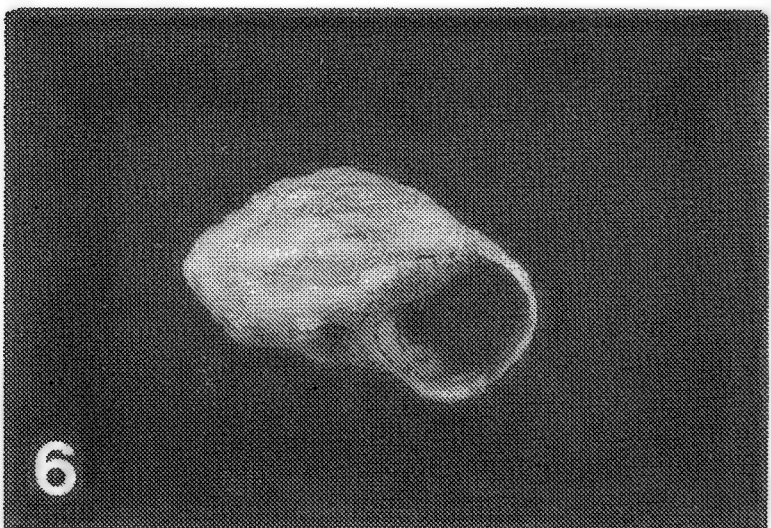
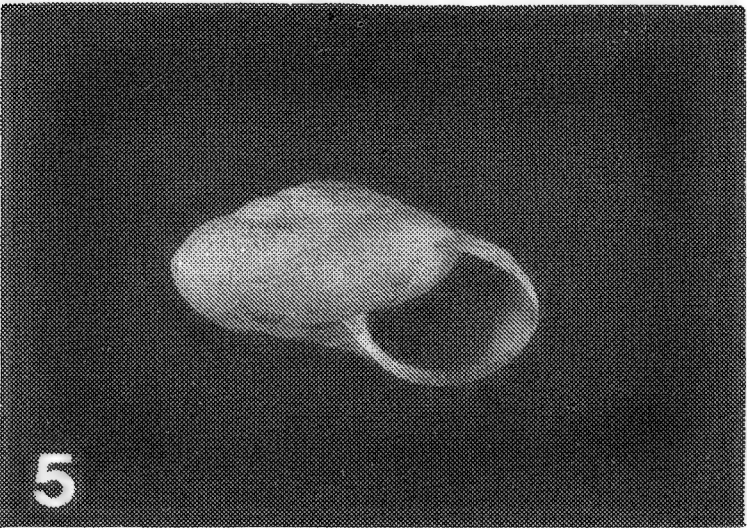
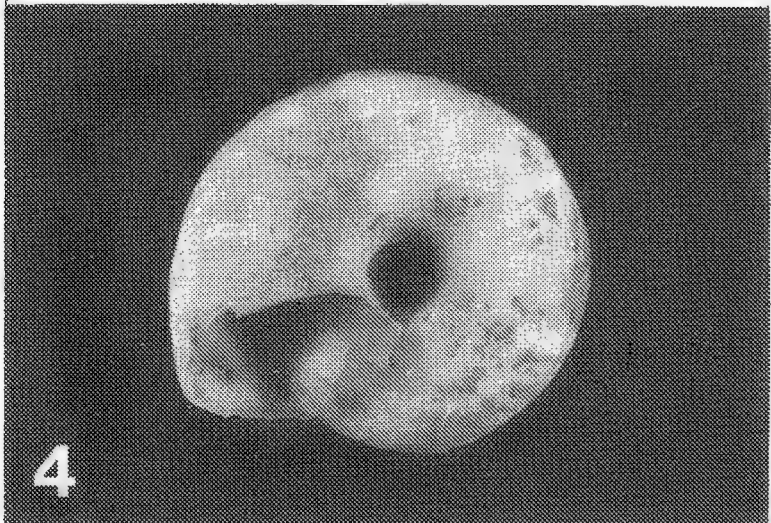
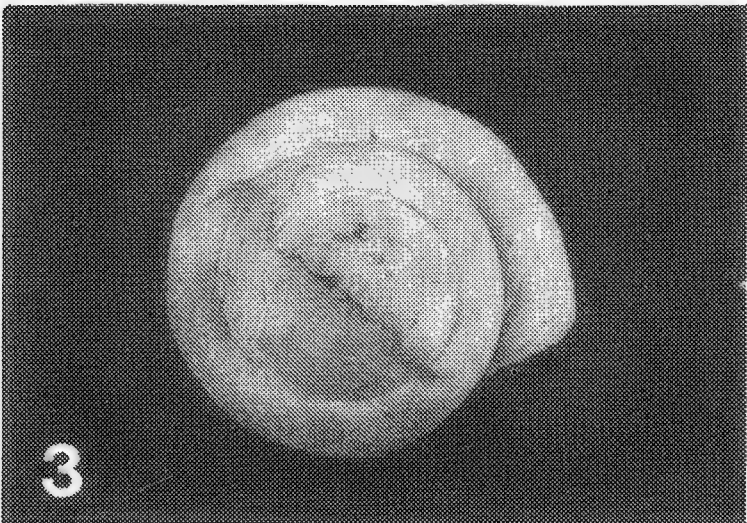
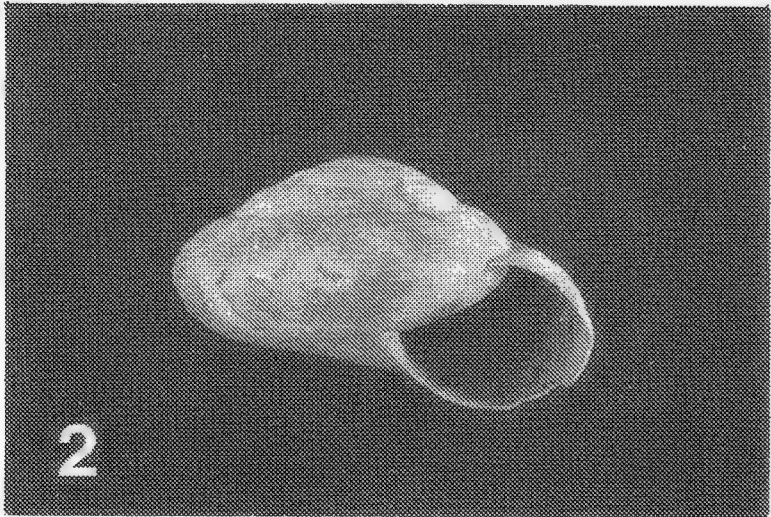
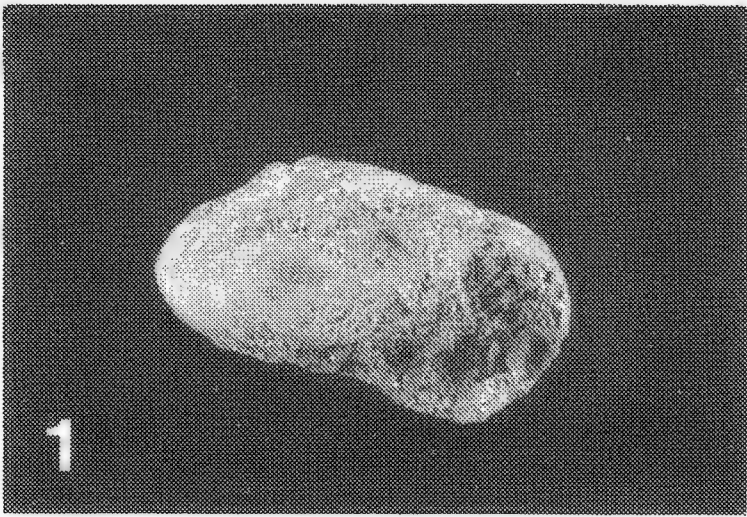
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## PLATE 31 (opposite)

*Zonites (zonites) santoriniensis* sp. nov.

Fig. 1, Paratype covered by calcrete. Figs. 2–4, Holotype. Figs. 5, 6, Sub-adult paratype. Fig. 7, Juvenile paratype. Fig. 8, Microsculpture (juvenile paratype). Photographs by T. Plodowski.









# CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND PROCEEDINGS

## REPORT OF THE COUNCIL 1986–1987

It was with a sense of shock that in May 1986 the President received the unexpected resignation of Dr. J. D. Nunn from the Office of Honorary Secretary. To cope with the emergency situation the President volunteered to be 'acting' Honorary Secretary until the Council could make other arrangements at the Annual General Meeting in March 1987.

The total membership of the Society now stands at 565. It is composed of the following categories:— *Full members* 428, *Full Life members* 32, *Family members* 36, *Family Life members* 6, *Junior members* 16, *Honorary members* 6, *Institutional members* 41 and *Subscribers* 147, a total of 565.

*New members nominated & elected March 1986–Feb. 1987*

*Full members* 33, *Family members* 1, *Junior members* 2, *Institutional members* 3.

*Resignations*

*Full members* 17, *Junior members* 1, *Institutional members* 1.

*Members struck off for non payments of subscriptions*

*Full members* 17, *Family members* 2, *Junior members* 2.

*Members 'lost' with no addresses*

*Full members* 4.

*Meetings*

There were 7 Ordinary Meetings held in the Demonstration Room of the British Museum (Natural History), and the Annual General Meeting, held in an empty gallery in the Museum. A Marine Workshop was held in the Humfrey Rooms in Northampton, by courtesy of the Northampton Natural History Society.

*Publications*

Two parts of the *Journal of Conchology* were issued (Volume 32, parts 3 and 4). Four issues of the *Conchologists' Newsletter* were printed and issued with the Annual Programme Card of events.

*Field Meetings*

Four field meetings were held during 1986. July 19th Folkestone, Kent. September 6th Sandwich, Kent. October 4th Market Weston, Suffolk. October 11th Folkestone, Kent. Thanks are due to the following for leading these meetings – Mr. S. P. Dance, Miss. J. Nelson, Mr. I. J. Killeen and Mr. E. Philp.

## TREASURER'S REPORT, 1986

The accounts for 1986 show a profit of £1,454.79, mainly due to the bequest of £1,000 from our late Member, Miss M. Jaques. There was also a considerable saving on the cost of the *Journal* – £5,084.17 as against £6,529.71 (which included the cost of covers for the current volume) for 1985, to which may be attributed the swing from the loss of last year.

Printing and postage costs were unusually high, but included the production of a new prospectus leaflet, new covenant forms and notices of the new subscription rates. The cost of meetings rose again due to the increased hire charges for the room, and it is probable that further increases in these may be expected.

There was a slight increase in Members' subscriptions, balancing a slight fall in the income from non-Member subscribers. The income from sales and from investments is very similar to last year's.

Covenanted subscriptions produced the addition of £258.29. This is very useful and the Society is grateful to all Members who have covenanted their subscriptions and hopes that others will consider doing this.

14 Ordinary Members, 2 Family Members and 3 Junior Members are in arrears with 1985 subscriptions. Members are reminded that no further publications will be sent to those whose current subscriptions remain unpaid. May I also remind Members of the new subscription rates – I have so far received over 70 subscriptions for this year at last year's rates: this is in most cases due to a failure to amend standing orders.

I regret that I am obliged to ask the meeting to accept the accounts subject to the Auditors' subsequent satisfaction. I was unable to entertain the Auditors as arranged because of sudden illness.

MARJORIE FOGAN  
Hon. Treasurer

#### RECORDER'S REPORT: MARINE MOLLUSCA

The tiny southern prosobranch *Paludinella littorina* is only recorded live from two places in Britain: Chesil Beach, Dorset, and the Isle of Wight (sea areas S16 Portland and S15 Wight). After a gap of a hundred years, live specimens have been rediscovered in 1986 at the Dorset site (Light, *J. Conch.*, **32** (1986) p. 260). It will be interesting to see whether it is still living in the Isle of Wight, where found in 1852 by Forbes and Hanley (*British Mollusca* **3** (1953), p. 265).

Also noteworthy is the report by Palmer (*J. Conch.* **32** (1986), pp. 258–9), of three deep water scaphopods from the Rockall Trough, new to the British Fauna.

Recording around Ireland has been much improved by the efforts of B. E. Picton, Dr J. D. Nunn and Dr S. M. Smith, particularly in the northwest, and in the course of investigations, mainly by University College, Galway, on the south coast. Among many interesting records, the following are rare or local in Britain and Ireland: *Eulima glabra* (da Costa), *Polygireulima (Balcis) sinuosa* (Scacchi), *Diaphana minuta* Brown, *Lepton nitidum* Turton, *Acanthocardia tuberculata* (L.). All are live, 1978 to 1981, from S38 Cork (*Proc. R. Ir. Acad.*, **86B** (1986) pp. 81–106).

D. R. SEAWARD

#### RECORDER'S REPORT: NON-MARINE MOLLUSCA

The following new vice-comital records have been verified since the last Report (*J. Conch.*, *Lond.* **32**, p. 252). All date from 1986–87.

Kent East (15): *Limax maculatus*, Folkestone (61/2236; garden), S. P. Dance.

Kent West (16): *Tandonia rustica*, One Tree Hill, Sevenoaks (51/5653), E. G. Philp.

**THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND**

**INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1986**

	£		£		£
Publications:—		Fees and Subscriptions:—			
Newletter .....		Membership Fees .....	4,963.67		
		Subscriptions .....	2,781.69		
		Entrance Fees .....	<u>39.00</u>		
Journal:—					7,784.36
Volume 32 No. 3 .....	2,422.91				
Volume 32 No. 4 .....	<u>2,661.26</u>				
Members' List .....		Donations .....		125.82	
Printing, Stationary and Postage ....		Bequest, Miss M. Jaques .....		1,000.00	
Officers' Expenses .....		Sales:—			
Meetings .....		Journal .....	34.01		
Subscriptions .....		Paper for Students .....	52.90		
Donation (Royal Society for		Special Publication .....	23.50		
Nature Conservation) .....		Atlas .....	18.00		
Bank Charges .....		Newsletter .....	15.60		
Marine Workshop .....		Boycott Papers .....	45.00		
		Other Publications .....	32.30		
		Record Cards .....	30.00		
		Shell Kit .....	10.00		
		Bookmarker .....	8.00		
		Advertising .....	<u>5.00</u>		
				274.31	
		Marine Workshop .....		50.30	
		Sales, Lemche Books .....		52.00	
		Investment Income:—			
		General Account .....	2,008.68		
		Life Members' Fund .....	402.42		
		Reserve and Research Fund .....	<u>382.40</u>		
Net Profit for the Year .....	1,454.79				
		Transfer to Reserve and	2,793.50		
		Research Fund .....	<u>382.40</u>		
				2,411.10	
				<u>£11,698.39</u>	



## BALANCE SHEET AS AT 31st DECEMBER, 1986

[illegible]

Suffolk East (25): *Boettgerilla pallens*, Woodbridge (62/2648); *Limax valentianus*, Ipswich (62/1843; garden), both I. J. Killeen.  
 Bedford (30): *Vertigo pusilla*, Tempsford (52/1851), Mrs E. B. Rands.  
 Gloucester East (33): *Arion fasciatus*, Edgeworth (32/9405), Mrs E. B. Rands; *Milax gagates*, Cheltenham (32/9420; garden), A. J. Rundle.  
 Gloucester West (34): *Arion fasciatus*, Tarlton (31/9599), Mrs E. B. Rands.  
 Radnor (43): *Limax tenellus*, Elan valley (22/9162), A. O. Chater.  
 Carmarthen (44): *Pupilla muscorum*, Tywyn Burrows (22/3605), I. K. Morgan; *Spermodea lamellata*, Nant Cwm-Hagr (22/3928), A. P. Fowles.  
 Cardigan (46): *Ena obscura*, Dovey Junction (22/6796), A. P. Fowles.  
 Merioneth (48): *Vallonia excentrica*, Aber Dysynni (23/5603), A. P. Fowles.  
 Leicester (55): *Milax gagates*, Burley on the Hill (43/8810), Mrs E. B. Rands.  
 Nottingham (56): *Arion flagellus*, Bingham (43/7039; garden), Miss S. M. Davies.  
 Lanark (77): *Arion hortensis* seg., Glasgow (26/5767; gardens), Miss S. M. Davies.  
 Berwick (81): *Deroceras caruanae*, Eccles (36/7641), Mrs M. Fogan.  
 Stirling (86): *Arion owenii*, Mugdock Reservoir (26/5675), Miss S. M. Davies.  
 Kincardine (91): *Deroceras agreste*, St. Cyrus N.N.R. (37/7463), A. O. Chater.  
 Aberdeen South (92): *Arion fasciatus*, Ballater (37/3795), A. O. Chater.  
 Aberdeen North (93): *Zonitoides nitidus*, Methick (38/8239), Mrs D. K. Marriott.  
 Kintyre (101): *Acicula fusca*, Taynish N.N.R. (16/7386), Mrs D. K. Marriott.  
 Caithness (109): *Sphaerium lacustre*, Rumuster Pond (39/2137), Melanie Spirit.

The most important find of the year is of yet a further species new to the British fauna: the milacid slug *Tandonia rustica* (Millet). An account of Mr Philp's discovery will be found on p. 302. It is unlikely that this highly distinctive slug has been overlooked in England; it must be genuinely rare here. The habitat, old calcareous woodland, is in keeping with the known requirements of the species abroad. It is locally common in Holland and Belgium, and its presence in the extreme south-east of England may represent an extension of its natural range rather than being due to recent introduction, especially as the species is not synanthropic.

Some other finds may be commented on as follows:

*Acicula fusca*. This is a very local snail in Scotland. The new site in Kintyre reinforces the known pattern of distribution at oceanic sites along the west coast.

*Vertigo pusilla*. A receding species, rarely found living in lowland England. The habitat at Tempsford (v.c. 30) was under bark of a dead elm.

*Arion hortensis* seg. This is the first record of authentic *A. hortensis* in Scotland. The species was found at two sites, on a river bank and in a garden. According to Stella Davies, in 1972 and in 1978 only *Arion distinctus* was apparently present in these places, suggesting a recent invasion.

*Limax maculatus*. The discovery of this species in some numbers in a garden in Kent is unexpected, as the known distribution is strikingly western. It is nevertheless likely that *L. maculatus* has been overlooked in synanthropic habitats in England, being confused with the commoner *Limax flavus* (see also *Conch. Newsletter* no. 97 (1986), p. 361).

*Limax valentianus*. Until very recently, this species was known in the British Isles only from glasshouses. Evidently it is now establishing itself in open situations. The latest find from a garden in Suffolk can be added to records at disturbed open sites in Bedfordshire and in Co. Dublin.

*Sphaerium lacustre*. This bivalve has essentially a lowland distribution in the British Isles; it is rare in Scotland, and scarcely known north of the Midland valley. The new site in Caithness is a marshy pond. A small globular form of the species was very common.

M. P. KERNEY

## COMMUNICATIONS

### NEW RECORDS OF MARINE MOLLUSCS IN THE FLEET, DORSET

During May and August 1969 my colleague John Whittaker made two surveys of the marine fauna of the Fleet at stations shown on Fig. 46 of Whittaker 1978 (*Proc. Dorset Nat. Hist. & Arch. Soc.* **100**, pp. 73–99). In May 1986 he invited me to examine the two collections and to report on the marine molluscs.

Examination of 138 tubes containing sedimentary and weed samples yielded 19 species for the May, and 30 for the August, Surveys. Of these, two were unpublished new records, while a third requires further collecting to confirm it.

Seaward (*Proc. Dorset Nat. Hist. & Arch. Soc.* **100** (1978) p. 108) listed 83 species from the Fleet, 67 living.

All stations of marine molluscs recorded below are in the SE. Fleet, between the Narrows and Ferrybridge.

**Ammonicera rota** (Forbes & Hanley, 1850): many specimens found at stns 20 (May) and 14, 19, 25, 42 (August), among sediment samples with weed. The largest was 0.7 mm across greatest diameter, the shells were fresh, unworn and looked as though they were alive when collected. Unlike most illustrations of *A. rota*, these were only lightly ribbed and with lateral spiral ridges instead of a peripheral keel. In this they more closely resembled *A. fischeriana* (Monterosato) from the Mediterranean. I am grateful to Stella Turk for confirming my tentative determination of this minute gastropod.

**Cingulopsis fulgida** (J. Adams, 1797): two specimens, 0.8 mm and 0.75 height, with typical blunt apices and two purplish-brown spiral bands on an ovoconic shell, were found at Stn 25 (August). The shells were bleached and with no sign of the operculum and dead when collected.

The *Helix fulgida* of J. Adams, 1797 was made the type species of *Cingulopsis* proposed by Fretter & Patil, 1958 (*Proc. Malac. Soc.* **33**, pp. 114–126) and removed from Rissoidae on the grounds of eight anatomical differences. A new family Cingulopsidae was proposed for this genus (*op. cit.*, p. 124). A third, but ambiguous, record is of an *Odostomia* which is neither *O. unidentata* nor *O. plicata* recorded by Seaward 1978 (*op. cit.*, p. 103); but which resembles juveniles of *O. scalaris* (= *O. rissoides*). The small size and single shell is insufficient to make a firm record.

Mention may also be made of three single valves, with periostracum, of *Pisidium subtruncatum* Malm, 1855 and *P. nitens* Jenyns, 1832; both found at stn 79 between the two streams emptying into Abbotsbury Swannery at the NW end of the Fleet.

Salinity at stn. 79 is 13‰ compared with 34‰ at SE end of the Fleet where a normal marine fauna is found. Both species are recorded by Kerney (1976 Non-marine Atlas) for the area so they are not new records. But, the presence of periostracum argues against transportation along a stream bed and raises the question whether they are living in 13‰ salinity in the NW end of the Fleet.

I am grateful to Michael Kerney for identifying these two species.

C. P. PALMER

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

(Received, 17th December 1986)

### REDISCOVERY OF *THEBA PISANA* AT MANORBIER, SOUTH WALES

*Theba pisana* (Müller) is a locally abundant land snail of Mediterranean coastal habitats, but whose range extends northwards as far as Britain where it is known from a few scattered localities in the south-west. In 1979 Cowie (*Ph.D. Thesis* (1982) Liverpool University; *Nature in Wales, New Series* **4** (1986) pp. 66–70) carried out a survey of its mainland British distribution, concentrating on the large but fragmented colonies in and around Tenby (South Wales). *T. pisana* has become less widely and more patchily distributed in this area since earlier records (especially Stubbs, *J. Conch.*, *Lond.* **9** (1900) pp. 321–328, 358–365) and it was suggested that this could be due both to urban development and increased tourism, and to short- and long-term climatic fluctuations. *T. pisana* was noted as absent from Manorbier, 8 km west of Tenby, where it had previously been recorded (Jeffreys, *British Conchology* (1862) London; Tye, *Quart. J. Conchol.* **1** (1877) pp. 230–233; Stubbs, *J. Conch.*, *Lond.* **9** (1900) pp. 321–328, 358–365; Deblock, *Diplome d'études supérieures Thesis* (1962) Faculté libre des sciences, Lille). Small isolated populations at the edge of a species' climatically-determined range would be particularly susceptible to short-term climatic fluctuations such as an especially cold winter, and this was put forward as a possible reason for its apparent extinction at Manorbier.



## COMMUNICATIONS

Since the 1979 survey a number of visits have been made to Manorbier and neither live individuals nor empty shells were found. However, in July 1986 a small population was discovered in dune beside the path leading from the car park to the beach of Manorbier bay. This population covered an area of about 100 square metres and probably contained about 2000 individuals. (This is a rather lower population density than often found in parts of the Tenby colony – Cowie, *J. anim. Ecol.* **53** (1984) pp. 311–325). Further searching revealed no other populations in the area. The snails found all had fully five-banded shells as in all Dyfed populations except those at Tenby itself (which have unbanded shells as well), and closely resembled these other five-banded shells in the style of the banding (see Cowie, *Malacologia* **25** (1984) pp. 361–380).

It is highly unlikely that this population was overlooked during previous visits to Manorbier, as it is adjacent to the main path to the beach. It is possible, however, that *T. pisana* was present in small numbers throughout this time in nearby areas, and that conditions suddenly became more amenable to its survival and increase; its potential for rapid population expansion is immense (Cowie, *J. anim. Ecol.* **53** (1984) pp. 311–325). A similar apparent absence and subsequent 'rediscovery' were reported by Turk (*J. Conch., Lond.* **26** (1966) pp. 19–25) for the St. Ives, Cornwall, colony of *T. pisana*, and a recently discovered colony which may in fact have been present in low numbers for many years was reported from near Padstow in Cornwall by Humphreys *et al.* (*J. Conch., Lond.* **31** (1982) p. 73).

It is also possible that *T. pisana* did become extinct at Manorbier and that it has been re-introduced. It is extremely easily transported on cars, picnic baskets, children's buckets and spades, etc., and just a few individuals brought in from Tenby would have the reproductive capacity to generate a large, flourishing population in just two or three years.

In some cases it is possible to discount persistence of a population at a very low level if shell morphs present in the current population were absent in the previous one. This is probably the case for the recent (1985) discovery of *T. pisana* in California. Shell morphs present now were absent from the introduced populations in the same area sampled during the early part of this century; the eradication campaign against *T. pisana* was probably successful (Armitage, *Calif. Dept. Agric. Bull.* **38** (1949) pp. 157–216) and the recent population is probably the result of a new introduction (D. S. Woodruff & R. H. Cowie, in preparation). Similarly, it may be possible to discount a particular provenance of a new introduction if morphs present in the introduced population are not present in the proposed progenitor population: *T. pisana* was probably not introduced to Treynon Bay (Padstow) from the St. Ives colony (Turk, *J. Conch., Lond.* **31** (1984) pp. 263–280). Unfortunately no specimens are available from the previous Manorbier colony, and shell morphs in the present population are common at Tenby and in the other South Wales localities. It is thus not possible to state that this 'rediscovered' colony is a new introduction and that *T. pisana* did go extinct at Manorbier, nor to say anything about its likely provenance (if it is a new introduction) except that it was probably introduced from somewhere in South Wales.

This rediscovery of *T. pisana* at Manorbier once again emphasizes the tenuous nature of populations at the edge of a species' range, their potential for rapid expansion and contraction, and the likelihood of frequent extinction and recolonisation. It will be interesting to follow the future course of this colony.

ROBERT H. COWIE

Tropical Development and Research Institute, College House, Wrights Lane, London W8 5SJ.  
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## CHARONIA LAMPAS (L.) LIVING OFF DOVER

Between 1847 when Jeffreys recorded the species from the Channel Isles (Crowley, *J. Conch. Lond.* **25**, p. 17) and 1970 no living specimens or even shells of *Charonia lampas* were reported from the Channel Isles or from any area north of the Isles. From 1970 onwards there have been a spate of records from the Channel Isles (Brehaut, *J. Conch. Lond.* **28**, p. 41), S. W. Ireland (O'Riordan, *Ir. Nat. J.* **17**, p. 252; **18**, p. 237; *J. Conch. Lond.* **27**, p. 371; *Conch. Newsletter* No. 62, p. 22), off Cornwall (Turk, *J. Conch. Lond.* **29**, p. 30; *Conch. Newsletter* No. 76, p. 296). During 1986, the writer acquired three specimens, all found living and all from off the Dover coast at 51 N 1.30 E. They were taken in March and May by the Belgian fishing boat Z.66/Nelson and retrieved by crew member Lowyk Wilham who said that he had previously seen specimens in the same place eight years and 20 years ago. The shells measured 173 mm × 90 mm; 167 × 78 mm; and 215 × 118 mm, and they have been exhibited at a meeting of the Dutch Conchological Society. These finds are further evidence that the species is indeed extending its range northwards in a north-easterly as well as north-westerly direction.

JOOP DE LIGT

Gladiolenlaan 4 1731 XV Winkel, Netherlands

Communicated by Stella M. Turk, Reskadinnick, Camborne, Cornwall.

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LIVE *CIRCULUS STRIATUS* IN SOUTH DEVON

On the 27th February, 1985, I found a single live specimen of the small prosobranch *Circulus striatus* (Philippi, 1836), of shell diameter 1.8 mm, in red foliose and calcareous algae which I collected from rocks on the lower shore at Lannacombe Beach, South Devon (SX801370, 50°13'N:03°40'W, sea area 18).

*Circulus striatus* is rare, there being only four previous satisfactory reports of it in the Society marine census area, all from north and north-west Ireland: from Bundoran, Donegal (sea area 34), by Jeffreys (*British Conchology* **3** (1865) p. 315), who apparently only found the shell, since he described the operculum from French specimens; from Bartra Is., Mayo (sea area 34) and Portrush, Antrim (sea area 29a) by Marshall (*J. Conch.* **9** (1898) p. 69), presumably as empty shells; and four empty shells from Clew Bay, Mayo (sea area 35) by Colgan (*Proc. R. Irish Acad.* **31** (1911) p. 13). Colgan states that 'Clew Bay is but the fifth Irish station on record for this rare species', but I can only find the four mentioned above.

A record of live *Circulus striatus* found in south-west Cornwall (sea area 18), reported by Gardiner (*J. Conch.* **22** (1945) p. 148), was subsequently withdrawn (Fowler, *J. Conch.* **23** (1948) p. 13) when it was realised that they were actually fry of *Gibbula umbilicalis* (da Costa), to which there is a superficial resemblance. The retraction of this record was overlooked when the *Sea Area Atlas of Marine Molluscs* (Seaward 1982) was prepared, so that it was erroneously included for sea area 18 on map no. 125. This map should be further amended by transferring the S29 Clyde record to S29a Antrim (Portrush), and by adding the S34 Donegal Bay (Bundoran) record.

The Lannacombe example appears to be the first recorded occurrence in British mainland waters of this animal, which has seldom been seen alive, and whose anatomy was described in 1956 by Fretter (*Proc. zool. Soc. Lond.* **126**, pp. 369–381), from specimens obtained, still living, from the stomachs of the starfish *Astropecten* dredged off St. Jean-de-Luz. It may be that its presence around Britain and Ireland is occasional, depending upon settlement of larvae from the south, and that it does not breed here successfully. Fretter and Graham comment (Prosobranch Molluscs of Britain and Denmark, p. 229, Suppl. 6, 1978, *J. Moll. Stud. Lond.*), that the size of the protoconch suggests a prolonged larval life.

I am grateful to Dr V. Fretter and Mrs S. M. Turk for helpful discussion and for confirming my identification.

The small weed collection from Lannacombe contained a rich molluscan fauna. With the *Circulus* were the following species, all living: *Gibbula umbilicalis* (da Costa), *Littorina saxatilis* (Oliv.) s.l. (juv.), *L. mariae* Sacchi and Rastelli, *L. obtusata* (L.), *Cingula cingillus* (Montagu), *Onoba semicostata* (Montagu), *Rissoa parva* (da Costa), *Barleeia unifasciata* (Montagu), *Cingulopsis fulgida* (J. Adams), *Rissoella diaphana* (Alder), *Skeneopsis planorbis* (Fabricius), *Nucella lapillus* (L.), *Mytilus edulis* L., *Musculus discors* (L.), *Lasaea rubra* (Montagu), and *Turtonia minuta* (Fabricius).

D. R. SEAWARD

Barn Court, Hamlet, Chetnole, Sherborne, Dorset, DT9 6NY.

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## GRAPHIS ALBIDA IN SOUTH DEVON

Although the small prosobranch *Graphis albida* (Kanmacher, 1798) is recorded from nearly all (30) of the coastal sea areas around Britain and Ireland, most of these records refer to empty shells. Of the few, scattered, live reports, only two are post-1950, one being of a specimen found in 1970 by P. G. Moore in a *Laminaria hyperborea* holdfast in sea area 9, Northumberland (Turk, *J. Conch. Lond.* (1974) **28**, p. 260). The other emerged from red algae which I collected from LWST on the shore at Teignmouth, South Devon (SX941719, 50°32'N:03°29'W, sea area 16 Portland), on 24th April, 1982.

When I examined the live animal, I had no descriptions available, and was surprised by the extraordinary shape of the foot, the front corners of which are produced into long recurved processes, reminiscent of some of the aeolid sea-slugs, these continually 'rippling' over the substrate as the animal crawls; my notes add 'crawls fast'. The large black eyes within the bases of the tentacles are also prominent.

Jeffreys (*British Conchology*, **4** (1867) p. 100) quotes Clark's description of an animal from Exmouth, South Devon; the foot was "greatly hollowed out in front and deeply labiated, having distinct, long, arched, linear auricles, which play or vibrate when the animal is crawling".

The species is probably overlooked because of its small size. The Teignmouth example had a shell length of 1.75 mm, and was found by vigorously shaking the weed in fresh water, which was immediately drained off and replaced by cold, well-aerated sea water. Operculate gastropods usually survive this treatment with no sign of distress.

D. R. SEAWARD

Barn Court, Hamlet, Chetnole, Sherborne, Dorset, DT9 6NY.

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# LASAEA RUBRA IN AN UNUSUAL HABITAT, IN THE FLEET, DORSET

The small bivalve *Lasaea rubra* (Montagu) is usually described as living on exposed rocky shores in crevices or in shelter such as empty barnacles or tufts of *Lichina* lichen, particularly in the splash zone (e.g., Tebble (1966) *British Bivalve Seashells*, p. 84), though Bouchet, Danrigal and Huyghens (*Living Seashells*, Poole, (1979), translated by B. E. Picton), mention (p. 88) that it is 'also found under scarcely humid stones on the saltmarsh', and refer to these as 'harsh environments'. Seed and O'Connor (*J. moll. Stud.* (1980) **46**, p. 66) say that '*Lasaea* exhibits a remarkable array of structural, behavioural and physiological adaptations which enable it to survive in the exceedingly harsh conditions of the high intertidal zone'.

In the lower Fleet in Dorset (Sea Area 16 Portland, 30(SY)67), *Lasaea* is abundant in a very different and apparently benign habitat, where the shingle of Chesil Beach descends into the sheltered water of the Fleet lagoon, with a tidal range of less than two metres and very little wave action. In places, as the tide ebbs, water issues from the shingle as 'springs' from mid-tide level downwards, deriving presumably from percolation from the sea or from high-tide storage in the shingle, being about the same salinity as the sea or the Fleet, which here is virtually marine. In this position, *Lasaea* is present in large numbers a few centimetres deep in the interstices of the shingle, continuously bathed in sea water, in an interesting community of molluscs and other phyla, including species normally sub-littoral (Seaward, (1985) *Conchologists' Newsletter* 95, pp. 322-3, and (1986) *Porcupine Newsletter* **3** (6), p. 142).

*Lasaea* also occurs in 'springs' further up the Fleet in its middle section (30(SY)68), but here the tidal range is only a few centimetres, the 'springs' flow intermittently, and the animals experience periods of emersion. More *Lasaea* are found in the 'salt-marsh' situation among rotting vegetation under stones with *Truncatella subcylindrica* (L.) and *Ovatella myosotis* (Draparnaud), where they are moist but may be out of water for several days. Salinity here is typically 20% to 30%.

The Fleet population of *Lasaea* is of the pale creamy-yellow variety.

D. R. SEAWARD

Barn Court, Hamlet, Chetnole, Sherborne, Dorset, DT9 6NY.

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## THE GENERIC CLASSIFICATION OF BRITISH MILACIDAE

Historically, most British authors have used the generic name *Milax* for all the Milacidae recorded from the British Isles, whilst continental workers separated these species into two genera, *Milax* and *Tandonia*. The separation of the two genera is, however, a complex problem on both nomenclatural and anatomical grounds.

Anatomically the genus *Tandonia* is separated from *Milax* by the following characters:

- The absence of a stimulator in the atrium of *Tandonia*
- The accessory glands enter the vagina in *Tandonia* and the atrium in *Milax*
- The atrium is small in *Tandonia* and much larger in *Milax*

The stimulator, described as occurring within the atrium of *sowerbyi* by Quick (*Bull. Brit. Mus. (Nat. Hist). Zool.* **6**, p. 158) and illustrated by British authors, would, at first sight, seem to place *sowerbyi* within the genus *Milax*. However, the accessory glands enter the vagina in *sowerbyi*, and not the atrium as they would if it belonged to this genus. In the Milacidae the term stimulator should be confined to the atrial organ in to which the atrial accessory glands open. Wiktor, (*Malak, Abh.* **7** (1981) pp. 143-145) 'found that the commonly repeated information on the atrial stimulator in *Tandonia sowerbyi* (Férussac, 1823) in fact refers to the big vaginal papilla.' Wiktor (pers. comm.) states that the anatomical terminology for this structure has not been established, in recent publications he uses the term 'tongue-like structure or fold', and the purpose of the structure is unknown. It is a matter of conjecture, but it may be used to close the lumen of one of the atrial ducts during copulation. Apart from *Tandonia sowerbyi* this structure, or a very similar one, is known at present only in the Turkish *T. pageti*.

The five British species should be listed as follows:

*Milax* Gray, 1855

*Milax gagates* (Draparnaud, 1801) (Type species)

*Milax nigricans* (Philippi, 1836)

*Tandonia* Lessona & Pollonera, 1882

*Tandonia rustica* (Millet, 1843) (Type species)

*Tandonia budapestensis* (Hazay, 1881)

*Tandonia sowerbyi* (Férussac, 1823)

The status of specific or generic names of slugs is often open to doubt because the types have been lost. Common usage has regarded *gagates* Draparnaud as the type of the genus *Milax*. Lessona & Pollonera (*Monogr. Limacidi Italiani*, Torino (1882) p. 54) wrote '*Questo sotto-genere ha per tipo l'A. marginata Drap. . . .*' The accompanying figure of *Amalia marginata* is obviously the slug now known as *Tandonia rustica*. Draparnaud's (1805) original description of *L. marginatus* could be identified with any of several species including *rustica* and *sowerbyi*; however, all indications would suggest that the author meant the species now known as *rustica*, the name *marginatus* being preoccupied by *L. marginatus* Müller, 1774, = *Lehmannia marginata* (Müller, 1774). In current literature *marginatus* Draparnaud, 1805 and *rustica* Millet, 1843, are considered to be synonymous. Since this is now widely accepted, and it cannot be ascertained which species was described by Draparnaud in 1805 it would seem unnecessary to change this usage.

I would like to thank Dr. Andrzej Wiktor for all his help in guiding me through the taxonomic minefield of the Milacidae.

A. NORRIS  
City Museum, Municipal Buildings, Leeds, LS1 3AA.  
(Received, 15th May 1987)

## NOTE

The index to volume **32** of the *Journal of Conchology* will be issued with volume **33**.

B. COLES  
Honorary Editor





## INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:— **Dr D. T. Holyoak, School of Geography and Geology, The College of St. Paul and St. Mary, The Park, Cheltenham, Gloucester, GL50 2RH.**

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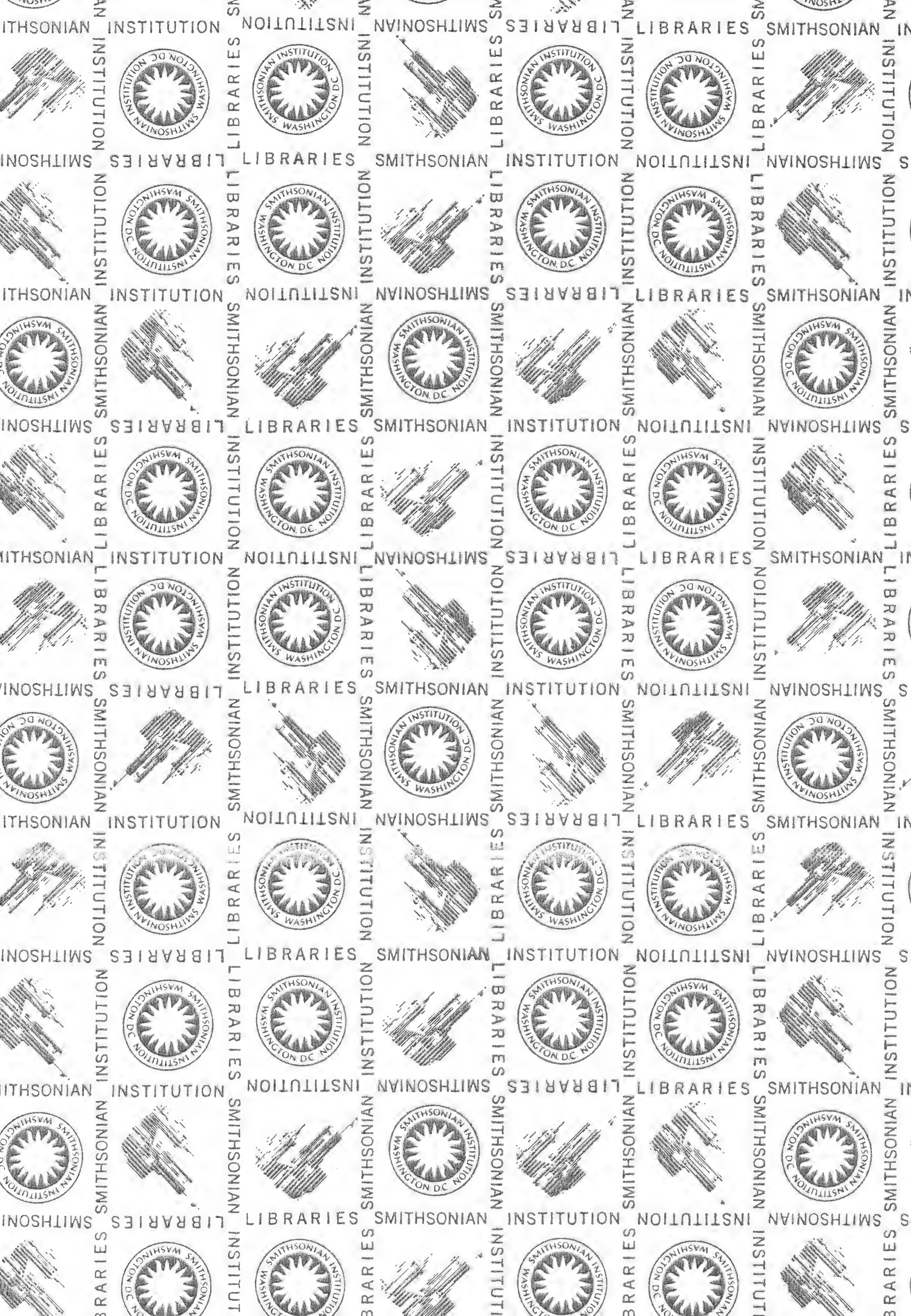
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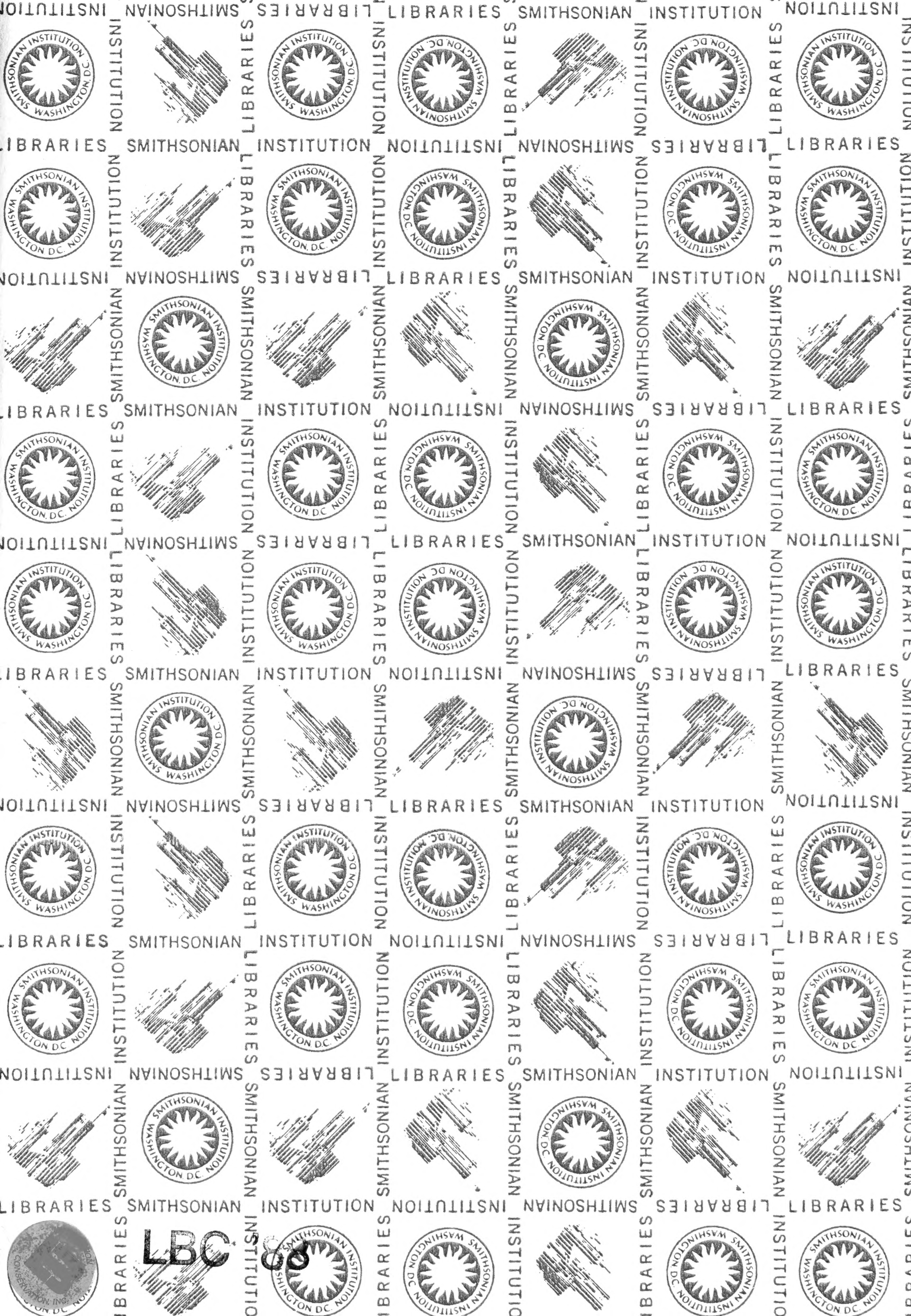
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ERRATA

Page 368, Table 3; the localities of *Vertigo genesii* (7) and *V. geyeri* (8) have been transposed.

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